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Interactions of Weed, Nematode, and Arthropod Management Strategies With the Louisiana Sugarcane Agroecosystem: A Holistic Perspective.

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Interactions of weed, nematode, and arthropod management strategies with the Louisiana sugarcane agroecosystem: A holistic perspective

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INTERACTIONS OF WEED, NEMATODE, AND ARTHROPOD MANAGEMENT STRATEGIES WITH THE LOUISIANA SUGARCANE AGROECOSYSTEM: A HOLISTIC PERSPECTIVE

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
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in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

Department of Entomology

by

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B.S., University of California at Davis, 1979

M.S., University of California at Davis, 1981

December 1987

PREFACE

"Every element of the physical reality must have a counter-part in the physical theory.

"In quantum mechanics in the case of the two physical quantities described by non-communicating operators, the knowledge of one precludes the knowledge of the other."

Einstein, A., B. Podolsky and N. Rosen. 1935. Can quantum-mechanical description of physical reality be considered complete? Physical Review 47: 777-780.

"Einstein, Podolsky, and Rosen's thought experiment is the Pandora's Box of modern physics."

Zukav, G. 1979. The dancing wu li masters: an overview of the new physics. William Morrow & Company, New York. 341 pp.

"Quantum phenømena provide prima facie evidence that information gets around in ways that do not conform to classical ideas. Thus the idea that information is transfered superluminally is, a priori, not unreasonable."

Stapp, H. P. 1977. Are superluminal connections necessary? Il Nuovo Cimento 40B: 191-205.

"Thus, one is led to a new notion of unbroken wholeness which denies the classical idea of analyzability of the world into separately and independently existent parts..."

Bohm, D. J. and B. J. Hiley. 1975. On the intuitive understanding of nonlocality as implied by quantum theory. Foundations of Physics 5: 93-109.

"In all of the Oriental religions great value is placed on the Sanskrit doctrine of Tat tvam asi, 'thou art that,' which asserts that everything you think you are and everything you think you perceive are undivided. To realize fully this lack of division is to become enlightened."

Pirsig, R. M. 1974. Zen and the art of motorcycle maintenance: An inquiry into values. Bantam, New York. 373 pp.

Agroecosystems are arbitrarily separated portions of the universe. As a part of the universe, an agroecosystem should be viewed from a holistic perspective to fully appreciate its inherent complexity.

ACKNOWLEDGMENTS

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My gratitude is extended to Dr. V.S.V. Rao of the Louisiana State University Biomchemistry Department for high performance liquid chomatography analyses of sugarcane free amino acids; to Mr. M.V. Patel of the Mississippi State University Plant Pathology Extension Service for assistance with nematode analyses of soil samples; to Dr. A.M. Golden of the USDA, Beltsville, Maryland, for nematode species identifications; to Dan Van Gent of the Louisiana State University Nuclear Science Center for invaluable assistance in the processing of the fire ant samples for neutron activation analysis and the volumes of raw data; and to John Krohn of the Texas A&M Nuclear Science Center, College Station, Texas, for reactor and semiconductor detector operation.

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I would like to express my thanks to Louisiana State University for bestowing upon me a Distinguished Alumni Federation Fellowship, which was both a great honor and sustenance for the duration of my doctoral studies.

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Finally, my appreciation to my sister, Dr. Linda A. Showler, for her moral support, and to Robert S. Showler, for his comaraderie, generosity, and brotherhood, and most of all, to my father and mother, Mr. and Mrs. Donald H. and Gloria A. Showler, who will always have my deepest love, respect, gratitude, and devotion for all that they are as individuals and parents until the end of time.

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ABSTRACT

Interactions among Louisiana sugarcane (Saccharum hybrids), weeds, nematodes, sugarcane mosaic virus (SCMV), and pest, prey, and predatory arthropods were mediated through trophic, host plant biochemical, and intra- and interspecific competitive relationships. Weed competition reduced crop biomass (15%, $P \leq 0.01$), stand density (18%, $P \leq 0.005$), and sugar yield (13%, $P \leq 0.05$). Weeds, however, were associated with more predatory arthropods, including Solenopsis invicta Buren, on the soil, weeds, and sugarcane plants, and with reduced Diatraea saccharalis (F.) injury (over 25%, $P \leq 0.05$). Without chemical D. saccharalis control, sugarcane production in weedy habitats was economically superior to that in weed-free habitats. Aldicarb, a nematicide-insecticide, diminished many phytophagous nematodes during the growing season, and reduced stalk-associated predators; thus, D. saccharalis injury increased by 19% ($P \leq 0.05$). Fenvalerate, a pyrethroid insecticide, reduced prey and predatory arthropods, increased Sipha flava (Forbes) infestations (63%, $P \leq 0.0001$), but provided over 70% control of D. saccharalis. Release of the crop from weed and D. saccharalis pressures was the most profitable pest management strategy.

Weeds were associated with low nematode infestations and, except for Criconemella spp., failed to reservoir phytophagous nematodes. Fifteen of 17 sugarcane free amino acids (FAAs) were lower ($P \leq 0.05$) where weed competition occurred. Nematode-induced stress was associated with the reduction of four FAAs ($P \leq 0.005$), and SCMV was related to other FAA changes. A weed-virus interaction ($P \leq 0.001$) for free cysteine was correlated ($r=0.59$, $P \leq 0.001$) with Tylenchorhynchus annulatus

infestations. Population trends of various nematode groups were also associated with virus, weed, and nematode stress-related FAA changes. Changes in sugarcane FAA accumulations may influence levels of other phytophagous pests, including nematodes.

Ecological interactions of S. invicta in North America, and the versatility of radiotracer methods for studying insect ecology and ethology were reviewed. Using radiotracers Zn-65 and Mn-54 to label two adjacent S. invicta colonies, the observation of daily territorial changes offered a unique perspective in association with environmental changes (including flooding) and colony behavior such as nest relocation. Utilizing instrumental neutron activation analysis and the tagging of S. invicta colonies with samarium, a rare earth element, revealed a 28% ($P \leq 0.02$) decrease in the size of S. invicta foraging areas due to greater food availability in weedy as compared to weed-free habitats. S. invicta foraging activity was negatively correlated ($r=-0.69$) with that of Paratrechina vividula, one of two other ant species encountered.

INTRODUCTION

Weeds have traditionally been regarded as competitors with crop plants (Harper 1977), hosts for microbial and arthropod pests (Altieri et al. 1977, Foster and Ruesink 1984), and obstructions to harvest operations (Fisher et al. 1977, AliNiazee et al. 1979, McWhorter and Anderson 1980). Recent studies, however, have indicated that indigenous weed communities, by supporting arthropod complexes that suppress key insect pests (AliNiazee et al. 1979, Altieri et al. 1977, Altieri 1980b, Altieri and Whitcomb 1979a,b), may play an important role in the productivity of agroecosystems. Most agricultural weeds are annual species that possess lesser competitive qualities than perennial species such as johnsongrass, Sorghum halepense L. Prudent management of annual weeds has been shown to result in a subcompetitive ground cover to enhance ecosystem stability and natural protection of various crops (Altieri 1980b, Altieri and Whitcomb 1980b).

Sugarcane (interspecific hybrids of Saccharum species), a perennial crop, is debilitated by stresses in addition to insect herbivory and weed competition. Plant-parasitic nematodes are wide-spread among cultivated soils and can persist from season to season on crop roots, weeds, plant debris, and even unvegetated soil (Ayoub 1980, Kenaga et al. 1971). By feeding through stylets, nematodes cause direct mechanical injury, including the reduction of feeder roots, galling, and tissue destruction that may inhibit physiological processes of the host plant, such as water and nutrient uptake (Astudillo and Birchfield 1980, Ramirez 1981), and indirect injury by vectoring plant viruses (Frazier

1970). Nematode-induced stress can precipitate changes in host plant biochemicals that have a role in the mediation of plant susceptibility to other pests (Noling et al. 1987). Nematode interactions with plant pathogenic viruses, bacteria, and fungi have been reported on many crop plants (Eisenbick and Griffon 1987, Noling et al. 1987, Sikora and Carter 1987) including sugarcane (Apt and Koike 1962).

Nematode control practices in Louisiana sugarcane are limited to nematicide treatments, fallow-plowing, and crop rotation (Birchfield 1972); resistant cultivars have not been implemented (Birchfield 1984). The efficacies of nematicides have been documented (Birchfield 1969, Birchfield 1972, Ramirez 1981) and nematode control may retard the yield declines associated with successive ratoon seasons (Birchfield 1969).

Most weeds are known alternate hosts for many agriculturally important nematode species (Gaskin 1958, Golden and Birchfield 1965, Hogger and Bird 1974, Bendixon et al. 1980, Manuel et al. 1980). Although weed communities have been associated with high nematode levels on crop plants (McSorley and Campbell 1980), certain plant species may reduce infestations (Birchfield and Martin 1956, Miller and Ahrens 1969, Haroon and Smart 1980). Drought stress has been shown to alter host plant free amino acid (FAA) accumulations (White 1984); it is possible that weed-induced stress could cause similar biochemical changes in plants that may influence levels of other phytophagous pests, including nematodes (Noling et al. 1987).

The key predator of the sugarcane borer, Diatraea saccharalis (F.), in Louisiana sugarcane is the imported fire ant, Solenopsis invicta

Buren, (Negm and Hensley 1967, Reagan et al. 1972), which also feeds on numerous other arthropods and plant material (Wilson and Oliver 1969, Ali et al. 1984). Vegetatively diversified sugarcane habitats support more prey arthropods and S. invicta colonies than weed-free areas (Ali et al. 1984). Previous investigation of S. invicta foraging behavior has revealed that the imported fire ant is territorial (Wilson et al. 1971). Not established thus far is the effect of weed conservation and associated changes in prey availability on S. invicta territories and also the relationship of foraging areas to the potential of the ant as a natural enemy in agroecosystems (see Appendix A).

Radiotracer techniques are versatile and sensitive tools for the study of insect ethology and ecology (see Appendix B). Instrumental neutron activation analysis (INAA) (Wang et al. 1975, Knaus and Curry 1979, Knaus and Van Gent 1987) provides an alternative to the hazards and public concerns associated with the use of radioactivity in the ecosystem (Jenkins 1963), often without the sacrifice of radiotracer sensitivity (Wang et al. 1975). At the present time, however, INAA has received scant attention in entomology although the ability to label insects with rare earth elements has been demonstrated (Richardson 1969, Curtis et al. 1973).

The research reported herein was conducted:

I. to provide a more holistic perspective on the relationships among floral and faunal components of the sugarcane agroecosystem,

II. to assess the importance of phytophagous nematode infestation relative to the costs of broad-spectrum nematode control,

III. to explore the role of weeds on the enhancement of predatory arthropod fauna and the natural suppression of sugarcane borer injury,

IV. to examine contemporary integrated pest management (IPM) tactics in light of alternative pest management strategies,

V. to refine understanding of S. invicta territoriality and its relevance to sugarcane IPM, and

VI. to demonstrate the practical use of stable-activable rare earth elements as alternatives to radiotracers for studies in agricultural systems that produce consumable crops.

LITERATURE REVIEW

I. VEGETATIONAL COMPLEXITY AND NATURAL ENEMY POPULATIONS IN SUGARCANE

Contemporary pest management strategies in Louisiana sugarcane involve the use of herbicides and insecticides. The study of arthropod interactions with weeds in agroecosystems is relatively new and has not been implemented as a component of IPM in sugarcane. Experiments regarding the effects of floral diversification on the enhancement of natural arthropod pest control, however, have produced noteworthy results.

Maize/bean polycultures were shown to sustain reduced injury by Diabrotica balteata LeCompte, Spodoptera frugiperda Smith, and Empoasca kraemeri Ross, as compared to corn monocultures (Altieri and Whitcomb 1980b). One modification of polycultural farming, termed "strip cropping," was instituted to accumulate natural enemy populations, portrayed by observations in strip-cropped alfalfa and corn (Laster 1974). The potential of floral manipulation has extended beyond the use of multiple crop species to the conservation of weeds in a corn/bean polyculture to increase the parasitism of S. frugiperda larvae (Altieri 1980b). Altieri (1980b) additionally found that a natural weed complex was more effective than a selected weed regime for the augmentation of beneficial arthropods.

Altieri and Whitcomb (1979a, 1980a) and Mangan et al. (1982) demonstrated that arthropod complexes are supported by indigenous weed species that may serve as reservoirs for beneficial insect populations in agricultural systems. Natural weed communities in crop monocultures were found to harbor substantial natural enemy populations that were

associated with the suppression of key insect pests (Altieri et al. 1977, Altieri and Whitcomb 1979b,c, 1980b).

Charpentier et al. (1967) revealed that sugarcane fields with histories of light D. saccharalis infestations harbored greater predaceous arthropod densities than heavily infested fields. The importance of sugarcane borer predators has been assessed by Charpentier et al. (1967), Negm and Hensley (1969b), and White (1980) where beneficial arthropod levels were found to be correlated with SCB egg and larval mortality. Beneficial arthropods have been attributed with the ability to provide 25% D. saccharalis control in Louisiana sugarcane (Reagan 1980). Although Louisiana sugarcane production is adversely affected when weed infestations are unmanaged (Fontenot and Sanders 1981, Ali and Reagan 1985), sugarcane weeds have been shown to support insect complexes (Nagarkatti and Nair 1973, Tirado and DeMartinez 1977) and natural enemy populations (Ali et al. 1984, Ali and Reagan 1985) such as S. invicta, and other Formicid species, Araneae, Carabidae, Dermaptera, and Staphylinidae (Negm and Hensley 1969b, Adams et al. 1981, Ali and Reagan 1986). Further, annual weeds are less competitive with sugarcane (Ali and Reagan 1985) than perennials such as S. halepense (Fontenot and Sanders 1981, Ali et al. 1986).

II. THE INFLUENCE OF BROAD-SPECTRUM NEMATICIDE/INSECTICIDES ON SUGARCANE ARTHROPODS

Nonselective and persistent pesticides such as Mirex and heptachlor have been shown to disrupt trophic webs and, consequently, D. saccharalis injury to sugarcane increased (Long 1958, Charpentier

et al. 1967, Negm and Hensley 1967, Negm and Hensley 1969a) by as much as 69% (Reagan et al. 1972). Aldicarb, a systemic carbamate reported to improve sugarcane yield (Birchfield 1971) and to control phytophagous nematodes (Waraitch 1982), has been associated with diminished predator arthropod levels in sugar beets (Gregoire-Wibo and Van Hoecke 1979) and cotton (Scott et al. 1985). The lethal effect of broad-spectrum pesticides on beneficial arthropods has been a reason for discouraging their use in an effective sugarcane pest management program (Reagan 1982).

III. THE USE OF SELECTIVE INSECTICIDES FOR THE CONTROL OF *DIATRAEA SACCHARALIS* IN LOUISIANA SUGARCANE

Louisiana sugarcane IPM tactics stress the importance of natural enemy conservation practices for more cost-effective and environmentally sound sugarcane borer control in addition to the use of selective, well-timed insecticide applications (Reagan 1982). The antiacetylcholinesterase compounds, monocrotophos, carbofuran, and methyl parathion, were, after repeated use against Texas-raised sugarcane borer populations, demonstrated to lose effectiveness by as much as 9-, 12-, and 8-fold, respectively (Reagan et al. 1979). Vines et al. (1984) found that, over twelve successive generations of chemical exposure, Louisiana *D. saccharalis* populations showed 3.6- and 7.6-fold resistance to fenvalerate and monocrotophos, respectively, and the fenvalerate-selected colony displayed cross-resistance to other pyrethroids including cypermethrin, flucythrinate, and permethrin.

Fenvalerate, however, has been reported as being less toxic to nontarget sugarcane arthropods (Hensley et al. 1981) and at least as

effective for control of D. saccharalis (Reagan et al. 1979, Showler et al. 1987) as the traditionally used azinphosmethyl. Fenvalerate use has been associated with reduced populations of Dermaptera and Gryllidae in sugarcane; Araneae, Carabidae, Cicindelidae, and Staphylinidae levels were not suppressed (Reagan 1980).

IV. THE EFFECT OF ALDICARB AND NEMATODE-INDUCED STRESS IN SUGARCANE

Birchfield (1984) reported that sugarcane, one of the first plants found to host plant-parasitic nematodes, was shown to harbor at least 14 phytophagous genera, including Meloidogyne, Pratylenchus, Trichodorus, and Tylenchorhynchus. Sugarcane yields have increased where aldicarb (Birchfield 1969), a plant systemic (Steele 1979), broad-spectrum oxime carbamate with a soil residual of about 10 weeks (Elliott et al. 1984), was used. Aldicarb may have variable effects on different nematodes (Hough and Thomason 1975, Huang et al. 1983); the nematicide was reported as being effective against Pratylenchus and Tylenchorhynchus spp. on corn (Williams and Beane 1984), Pratylenchus spp. on barley (Saynor 1979), Tylenchorhynchus and Helicotylenchus spp. on Lolium spp. (Spaull et al. 1985), Heterodera and Pratylenchus spp. on soybeans (Minton et al. 1985), and Pratylenchus penetrans on beans (Elliott et al. 1984) but not against Longidorus elongatus on ryegrass, swede, carrot, pansy, barley, and potatoes (Trudgill et al. 1985); Criconemella, Pratylenchus (Spaull et al. 1985), and Longidorus (Boag 1984) on Lolium spp.; Globodera rostochiensis on potatoes (Trudgill et al. 1985) and Pratylenchus, Longidorus, and Tylenchorhynchus on swede (Alphey and Boag 1979). Other studies have indicated that aldicarb, instead of being lethal to phytophagous nematodes, may only interfere

with nematode orientation and migration in the soil (Hough and Thomason 1975, Huang et al. 1983, Trett and Perry 1985). Rickard (1973) found that aldicarb-treated soil was rapidly re-established by Trichodorus christei. Detailed reports of nematode population dynamics in sugarcane, however, have not been available prior to the studies described herein.

The review by White (1984) on stress-induced changes in plant free amino acid (FAA) concentrations indicated that FAA levels may be linked with plant resistance to phytophagous organisms. Altered host plant FAA accumulations have been recorded from Meloidogyne incognita galls on tomatoes (Myuge 1956), Ditylenchus dipsaci-infested alfalfa (Howell and Krusberg 1966), Longidorus africanus-infected grapevines (Epstein and Cohn 1971), Meloidogyne incognita-infected tobacco (Hanounik and Osborne 1975), and Aphelenchoides ritzemabosi-infested alfalfa (Krusberg 1961). Hanounik and Osborne (1975) postulated that nematode injury to roots may influence host plant biochemical processes by interfering with the site of biochemical synthesis. Other studies, however, indicated that proline is critically important to the formation of cell wall proteins (Thimann 1972) and the reparation of damaged xylem elements (Roberts and Baba 1968). Owens and Sprecht (1966) found that FAAs were produced in nematode gall tissues, while Bird and Loveys (1975), using $^{14}CO_2$, determined that Meloidogyne javanica on tomato roots were sinks for photosynthetic nutrients, especially during egg production. Similarly, Meon et al. (1978) found that proline, a component of M. javanica egg shells (Bird and McClure 1976), increased with M. javanica infection levels on tomatoes, particularly when eggs were being formed. The relationship between nematodes and FAA accumulations is thus not clear

and, as Wallace (1983) stated, nematodes and other factors (to be discussed in section V of this leterature review) are inextricably linked and should be considered together.

V. WEED AND SUGARCANE MOSAIC VIRUS INTERACTIONS WITH SUGARCANE NEMATODE POPULATIONS

Nematode populations in agroecosystems have been described as being influenced by a plexus of environmental parameters (Wallace 1983) including initial phytophagous nematode abundances (Seinhorst 1965, Seinhorst and Kozlowska 1977, Ferris et al. 1981), organic soil content (Solhenius 1980, Peterson and Luxton 1982), tillage practices (Caveness 1974, Fortnum and Karlen 1985, Parmelee and Alston 1986), varietal resistance (Anzalone and Birchfield 1977, Niblack et al. 1986), the number of seasons a cultural regime has been used (Baird and Bernard 1984), the quality and availability of root space (Nusbaum and Ferris 1973, Barker and Olthof 1976), fungal-nematode (Jenkins and Taylor 1967, Ferris et al. 1981) and nematode-nematode interactions (Griffin 1980, Duncan and Ferris 1982), and insect herbivory (Noling et al. 1984).

Weeds have been shown to host phytophagous nematodes in many crop systems (Bird and Hogger 1973, Cooper and Harrison 1973, Hogger and Bird 1974, Minton et al. 1980); McSorley and Campbell (1980), for example, found intensified Pratylenchus brachyurus and Rotylenchus reniformis densities on avocado roots where weeds were not eliminated. Bendixon et al. (1980) and Manuel et al. (1980) published bibliographies that listed studies on weed hosts of phytophagous nematodes. Birchfield and Martin (1956) recognized S. halepense as a host of Tylenchorhynchus martini, both widespread pests of sugarcane. Golden and Birchfield

(1965) cited the presence of Meloidogyne graminicola on a common sugarcane weed, Echinochloa colonum (L.); Yik and Birchfield (1969) listed weeds parasitized by M. graminicola.

All weeds are not, however, favorable to plant-parasitic nematodes; some may even suppress nematode populations. Using steam-sterilized soil inoculated with Tylenchorhynchus martini, Birchfield and Martin (1956) concluded that sweet clover, Melilotus indica (All.) and Ligustrum vulgare (L.) reduced nematode populations. Marigolds, Tagetes spp., were shown by Miller and Ahrens (1969) to depress levels of Tylenchorhynchus claytoni and Pratylenchus penetrans. Similarly, Haroon and Smart (1980) interplanted tomato seedlings with pangolagrass, Digitaria decumbens (Stent), and found that M. incognita infestations were suppressed; root extracts of D. decumbens were observed to have ovicidal and larvicidal properties. The influence of weeds on sugarcane nematodes has not been addressed until the studies described herein were conducted.

Another poorly understood aspect of sugarcane nematology is the possibility of interactions with pathogenic microbes. Birchfield (1984) indicated that most Louisiana sugarcane ratoon stands harbor from six to eight phytophagous nematode genera, and the soil-borne fungi Pythium spp., Phytophthora spp., and Colletotrichum falcatum. On cotton, in the presence of Meloidogyne spp., even the most Fusarium wilt resistant varieties become susceptible (Birchfield 1984). Glomus intraradices colonization of cotton was associated with increased development of M. incognita (Smith et al 1986). Virus-infected plants have been shown to harbor fewer (Gosswami et al. 1974, Huang et al. 1984), or greater (Bird 1969, Taylor 1979) numbers of phytophagous nematodes than virus-free

plants. Apt and Koike (1962) reported synergistic sugarcane losses where Helicotylenchus nannus and Pythium graminicola were sympatric. Koike (1974) found that ratoon stunting disease in combination with SCMV, a wide-spread disease of Louisiana sugarcane, resulted in additive yield losses.

Changes in FAA concentrations have been associated with plant resistance to nematode infection in cotton (Lewis and McClure 1975), and virus infection has been shown to reduce (Cooper and Selman 1974), increase (Tu and Ford 1970, Lodh et al. 1971, Doke 1972, Ajayi 1986), or fail to affect (Gildow 1980) FAA accumulations in selected host plants. Information on the role of plant FAAs on nematode infestations is sparse; Bird (1959), however, found that tomato root exudates included glutamic acid, alanine, aspartic acid, serine, valine, phenylalanine, and cysteine, which was attractive to phytophagous nematodes in the soil. Although drought stress has been associated with changes in plant FAA levels, the interactions of weed competition and SCMV-induced stress with sugarcane FAA levels and phytophagous nematode populations have not been addressed.

VI. TERRITORIALITY AND FORAGING ACTIVITY OF SOLENOPSIS INVICTA AS DETERMINED USING RADIOTRACER AND INSTRUMENTAL NEUTRON ACTIVATION ANALYSES

The imported fire ant, Solenopsis invicta Buren, has been identified as being highly interactive with the ecosystem in the southeastern United States (Appendix A), and as an important predator of many agricultural pests (review: Reagan 1986) including D. saccharalis in Louisiana sugarcane (Negm and Hensley 1967, Reagan et al. 1972).

Ali et al. (1984) found that S. invicta colonies were more dense in weedy sugarcane habitats.

Territorial behavior has been identified in many ant species (review: Levings and Traniello 1981). Holldobler (1976) suggested that ant territories are composed of the nest and shifting foraging trails. Using differently colored dye markers ingested by selected fire ant colonies, Wilson et al. (1971) showed that S. invicta foraging areas were discrete but variable in size with seasonal changes. Radiotracer methodology has been applied to study insect ecology and ethology (Appendix B) including trophallactic (food exchange) behavior among S. invicta workers using I-125 (Howard and Tschinkel 1980, Sorenson et al. 1980), I-131 (Eisner and Wilson 1958), and P-32 (Gosswald and Kloft 1960, Naarman 1963, Bhatkar and Kloft 1977). Instrumental neutron activation analysis (INAA) (Knaus and Van Gent 1987) has received very little attention in entomology, although it has been shown that Drosophila spp. can be successfully labeled with dysprosium (Richardson 1971) and Glossina morsitans Westwood with europium, dysprosium, and gold (Curtis et al. 1973). The daily territorial dynamics of the imported fire ant and the influence of weed management practices on S. invicta foraging areas and activity have not been revealed by previous studies.

CHAPTER I

SUGARCANE BORER, WEED, AND NEMATODE CONTROL STRATEGY INTERACTIONS WITH LOUISIANA SUGARCANE ARTHROPOD FAUNA AND YIELD

This chapter has been modified and submitted to Environmental Entomology as manuscript number 87-17-1569.

INTRODUCTION

Louisiana sugarcane may be adversely affected when weed (Fontenot and Sanders 1981, Ali and Reagan 1985b), nematode (Birchfield 1969), and sugarcane borer (SCB), Diatraea saccharalis (F.), (Reagan 1980, 1982) populations are unmanaged. A combination of pest problems, known as stubble decline, results in crop yields that progressively diminish with ratoon seasons. Management tactics usually involve cultivation and herbicide treatments for weed control, and up to four insecticide applications for SCB control when live larvae are found on five percent of the stalks (Pollet et al. 1978). Nematode control is not a traditional component of Louisiana sugarcane production.

Vegetatively diversified crop systems host a plexus of beneficial arthropods; thus weeds may play a productive role in agroecosystems (Altieri et al. 1977, Altieri and Whitcomb 1980, White 1980). Sugarcane weeds serve as reservoirs for prey items that help sustain dense SCB predator populations including the imported fire ant (IFA), Solenopsis invicta Buren, (Ali et al. 1984, Ali and Reagan 1985b) other Formicid species, Araneae, Carabidae, Dermaptera, and Staphylinidae (Negm and Hensley 1969, Adams et al. 1981, Ali and Reagan 1986). Furthermore, annual weeds in Louisiana cane fields are less competitive (Ali and Reagan 1985b) than perennials such as johnsongrass, Sorghum halepense L., (Fontenot and Sanders 1981, Ali et al. 1986).

Birchfield (1984) indicated that sugarcane was among the first plants reported to host injurious nematodes and has been shown to produce more biomass and extractable sugar where nematicides have been used (Birchfield 1969, Ramirez 1981). Showler et al. (1987b), however, observed that aldicarb provided inconsistent control of most

phytophagous nematode species on Louisiana sugarcane. Further, aldicarb use has been associated with reductions of predatory arthropods in cotton (Scott et al. 1985) and sugar beet (Gregoire-Wibo and Van Hoecke 1979) fields. Although most weeds in cultivated soils can host phytophagous nematodes (Hogger and Bird 1974, Manuel et al. 1980), Showler et al. (1987c) found that total plant-parasitic nematode populations tended to be lower in the cane rhizosphere in weedy habitats.

Louisiana sugarcane integrated pest management (IPM) tactics stress the enhancement of the natural enemies of D. saccharalis (Reagan 1982) and the use of selective insecticides. Fenvalerate was reported as being less toxic to nontarget arthropods (Hensley et al. 1981) and at least as effective for SCB control (Reagan et al. 1979, Showler et al. 1987a) than the traditionally used organophosphate, azinphosmethyl. This study was conducted to examine the impacts and interactions of annual weed populations, a nematicide-insecticide, and a more selective insecticide on sugarcane arthropod fauna and yield. Our goal was to delineate the interactions of selected IPM strategies with sugarcane arthropod fauna and yield.

MATERIALS AND METHODS

A plant and first ratoon sugarcane ('CP 74-383') field in Assumption Parish, Louisiana, was used in 1985 and 1986. The experiment was a randomized complete block design with a split-split plot arrangement of treatments (Appendix C). The 0.2 ha whole plots were either weedy (W) or weed-free (WF); these habitats were replicated 6 times. W habitats were spot-treated with dicamba (9.6 g ai/ha) as

dicot weeds emerged. WF habitats were treated in early May of each year with a tank mix of metribuzin (1.3 kg ai/ha) and dicamba + 2,4-D (1.3 kg ai/ha and 2.7 1 ai/ha, respectively) from a tractor-mounted boom sprayer. In midsummer, WF habitats were spot-treated with metribuzin (25.5 g ai/1). Johnson grass was systematically eliminated with spot-treatments of asulam (2% ai) and by hand-roguing. Sub plots, each 0.05 ha in area, were either treated with a soil-incorporated granular formulation of aldicarb (80 g ai/ha), an effective sugarcane nematicide (Birchfield 1971) (A=aldicarb- treated) or left untreated (C=no nematicide or check plot). Sub-sub plots, each 0.025 ha in area, were either sprayed (Solo backpack sprayer) with fenvalerate (0.16 kg ai/ha) when 5 percent of the examined stalks had live SCB larvae in the WC habitats or were left untreated (I=insecticide, NI=no insecticide). Thus, at the split-split plot level, eight experimental habitats were created: WC-NI, WFC-NI, WC-I, WFC-I, WA-NI, WFA-NI, WA-I, and WFA-I.

Total weed biomass was measured by taking five random 0.5-m^2 quadrats of foliage clipped to the soil surface (2 of which were partitioned by weed species) in May, August, and October of each season. All samples were dried for 48 h at 94°C, then weighed. Soil surface-associated arthropod fauna were sampled from July to October in both years with one pitfall trap (Greenslade 1964) per sub-sub plot, changed biweekly. Standard sweep nets (Rudd and Jensen 1977) were used to collect arthropods from the weeds and cane canopy, with 40 sweeps per sub-sub plot at two week intervals from late July to mid-August (3X) when weed density was high. Sweep net samples were placed in plastic bags and frozen until the arthropods were counted and identified. Live SCB larvae and stalk-associated predators were monitored biweekly, from

July to October, by inspection of the leaf sheaths of 10 stalks per sub-sub plot. IFA mounds were counted in each sub plot in August of 1985 and 1986.

Sugarcane harvest yields were determined by weighing 50 stalks with leaf sheaths removed (biomass) and by counting the number of stalks per 11 m of row within each sub-sub plot (density). Sugar content was calculated from 20 stalks per sub-sub plot as described by Meade (1964), and sugar yields were calculated with a computer-based program (Heagler et al. 1985). Data were subjected to appropriate ANOVA procedures (SAS Institute 1979) to delineate relationships and interactions among the weed, nematicide, and insecticide treatment factors.

Economic cost-benefit analyses of each treatment were based upon financial expenditures including chemical, labor, fuel costs (Appendix B), and SCB-induced sugar losses per ha. Return investment ratios (RIRs) were calculated to indicate net dollar gains or losses per dollar invested in the respective pest management strategies.

RESULTS

Digitaria sanguinalis Scop. alone comprised up to 88.7 percent of the total weed biomass. Total biomass (Table 1) was significantly greater in W habitats on every sampling date each year ($F=56.97, 127.24$; $df=1,5$; $P \leq 0.001, 0.01$; 1985, 1986) than in WF regimes, even when late season cane canopy closure shaded out most weeds (Fig. 1). Soil surface-, weed-, cane canopy-, and cane stalk-associated arthropod groups and their overall percent abundances (across both years and all treatment combinations) are presented in Table 2. We did not find any

Table 1. Biomass of annual monocot weed species in selected sugarcane habitats, 1985 and 1986.

	Weed biomass (g/0.5 m^2)									
Habitat[a/]	Brachyaria platyphylla		Cynodon dactylon		Digitaria sanguinalis		Echinochloa spp.[b/]		Panicum dichotomiflorum	
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
WFC	0	0	0	0	0.2	1.8	0	0	0.3	0
WC	1.7	3.4	4.2	2.8	94.8	37.4	3.0	0.6	3.2	0.7
WFA	0.1	0	0	0.1	0.4	0.3	0	0	0.5	0
WA	6.5	0	1.8	1.6	60.7	33.4	4.0	0.2	10.0	0.2
(SE)	(1.6)	(1.1)	(2.2)	(0.8)	(13.6)	(7.9)	(1.0)	(0.2)	(3.1)	(0.2)

a/ W=weedy, WF=weed-free; C=no aldicarb, A=aldicarb-treated.

b/ Predominantly E. colonum and may include E. crusgalli L.

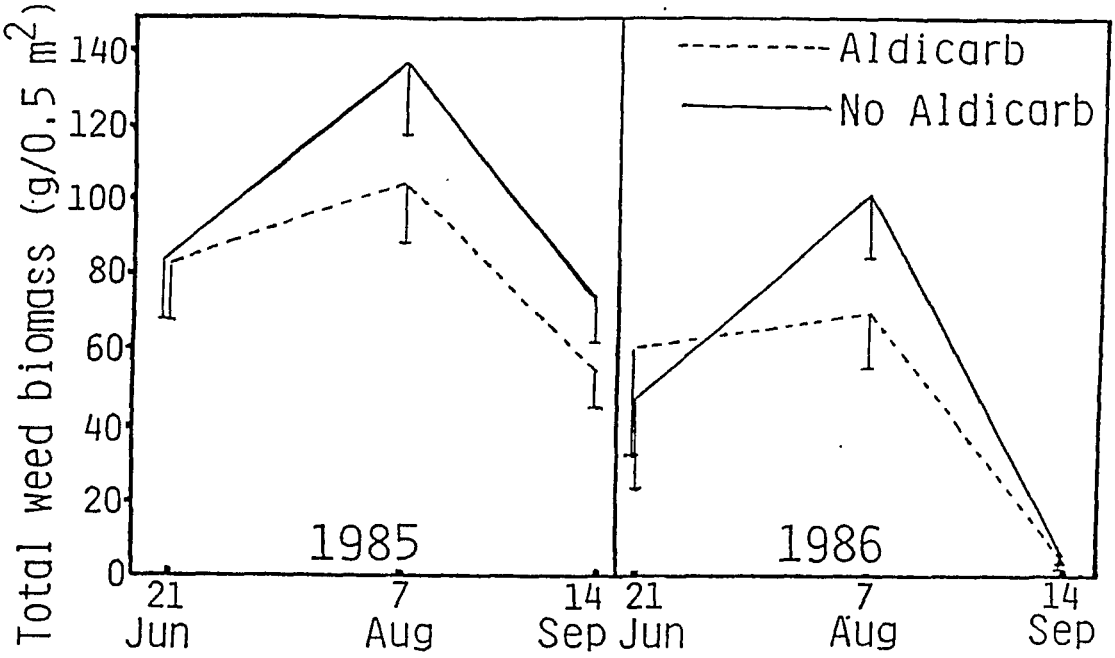

Fig. 1. Seasonal biomass (g/0.5 m^2-SE) of total annual monocot weeds (±SE) in weedy aldicarb-treated and aldicarb-free sugarcane habitats, 1985 and 1986. Differences ($P \leq 0.05$) in weed biomass between the nematicide treatments were not detected.

Table 2. Relative abundances of selected prey and predator arthropods found on the soil surface (ground), weeds, and cane foliage and stalks at Westfield Plantation, Assumption P., LA, 1985 and 1986.

Trophic level	Arthropod category[b]	Arthropod Abundance by Percent±SE[a] Ground-associated[c]	Weed-associated[d]	Cane foliage-associated[e]	Cane stalk-associated[f]
Prey:					
	Sucking Herbivores	25.0±2.88	67.6±6.13	90.8±2.69	none
	Lygaeidae	+	+	+	-
	Pentatomidae	+	+	+	-
	Aphididae	-	-	+	-
	Cicadellidae	+	+	+	-
	Chewing Herbivores	75.0±2.88	19.5±5.90	4.7±1.85	SCB[g]
	Chilopoda	+	-	-	-
	Orthoptera	+	+	+	-
	Chrysomelidae	+	+	+	-
	Curculionidae	+	+	+	-
	Other Coleoptera	+	+	+	-
	Lepidoptera larvae	+	+	+	+
	Diptera	uncounted	12.9±1.62	4.4±1.03	none
Predators:					
	Solenopsis invicta	31.3±2.95	43.4±5.04	19.4±6.40	61.5±5.41
	Other formicidae	0.7±0.12	7.0±2.46	5.2±1.34	27.0±4.04
	Paratrechina vividula	+	+	+	+
	Pheidole moerens	+	+	+	+

Table 2. (cont'd).

Trophic level	Arthropod category[b/]	Arthropod Abundance by Percent±SE[a/]: Ground-associated[c/]	Weed-associated[d/]	Cane foliage-associated[e/]	Cane stalk-associated[f/]
Predators: (cont'd)					
	Reduviidae	0.04±0.02	6.0±1.70	5.2±4.23	none
	Dermaptera	4.9±0.77	none	none	4.3±0.94
	Staphylinidae	2.0±0.37	none	none	2.7±1.18
	Carabidae	1.9±0.36	none	none	2.3±0.66
	Araneae	32.3±1.53	42.4±5.96	17.3±3.85	2.1±0.38
	Aranaeidae	-	+	+	-
	Clubionidae	+	+	-	+
	Linyphiidae	+	+	+	+
	Lycosidae	+	+	-	+
	Nesticidae	+	+	+	-
	Oxyopidae	+	+	+	-
	Pisauridae	+	+	+	+
	Salticidae	+	+	+	+
	Theridiidae	+	+	+	+
	Thomisidae	-	+	+	-
	Other predators	27.1±2.33	none	53.0±5.24	none
	Enicocephalidae	+	+	+	+
	Geocoris sp.	+	+	+	-
	Cicindelidae	+	-	-	-
	Coccinelidae	+	+	+	-

Table 2. (cont'd).

Trophic level	Arthropod category[b/]	Arthropod Abundance by Percent±SE[a/]: Ground-associated[c/]	Weed-associated[d/]	Cane foliage-associated[e/]	Cane stalk-associated[f/]
Predators: (cont'd)					
	Elateridae	+	-	-	-
	Parasitic Hymenoptera	+	+	+	-

[a/] Relative abundance data represents overall (1985 and 1986 combined) category means as a percent of the totals for prey or predatory arthropods.

+ = arthropod group present, - = arthropod group absent.

[b/] The insect and spider species encountered are included in the lists compiled by Ali et al. (1984) and Ali & Reagan (1985), respectively.

[c/] Based on pitfall trap counts (July-October).

[d/] Based on sweep net counts (July-August); no samples taken in weed-free habitats.

[e/] Based on sweep net counts (July-August).

[f/] Based on cane stalk and leaf sheath inspections (July-October).

[g/] SCB = sugarcane borer, Diatraea saccharalis F.

insect species beyond those listed by Ali et al. (1984) nor Araneid families outside of those recorded by Ali and Reagan (1985a). Numbers of ground-, weed-, cane canopy-, and stalk-associated arthropods in the eight sugarcane habitats are shown in Figure 2,A-E.

Weed Effects. Soil surface-associated prey arthropod (Table 2) populations (Fig. 2,A) were significantly lower (39.9%, 29.9%; F=33.26, 71.06; df=1,5; MSE= 50.5, 24.6; P≤0.002, 0.004; 1985, 1986) in the absence of weeds, as were both sucking (33.5%, 32.4%; F=16.96, 6.73; df=1,5; MSE=7.7, 7.0; P≤0.01, 0.05; 1985, 1986) and chewing (41.6%, 31.0%; F=24.09, 72.09; df=1,5; MSE=35.4, 16.1; P≤0.005, 0.0004; 1985, 1986) herbivores. Total soil surface-associated predaceous arthropods were diminished (41.1%, 29.9%; F=14.96, 25.26; df=1,5; MSE=663.9, 150.3; P≤0.02, 0.004; 1985, 1986) in WF plots; SCB predator groups reduced were S. invicta which had fewer mounds per ha (85.7%, 77.8%; F=60.00, 16.65; df=1,5; MSE=0.4, 10.9; P≤0.001, 0.01; 1985, 1986; Fig. 3) and soil surface-associated foragers (43.6%; F=8.11; df=1,5; MSE=262.2, 131.5; P≤0.04; 1985), Araneae (36.3%, 28.9%; F=9.18, 24.06; df=1,5; MSE=40.4, 14.6; P≤0.03, 0.004; 1985, 1986), and "other" predators (47.5%, 33.4%; F=13.29, 6.83; df=1,5; MSE=57.6, 18.0; P≤0.02, 0.003; 1985, 1986).

Weed-associated arthropods (not in the WF habitats) were found in high numbers relative to populations on the cane foliage (Fig. 2,B-C). Both cane foliage-associated sucking herbivores (42.2%: F=24.58; df=1,5; MSE=23.7; P≤0.004; 1985) and dipterous prey (58.0%, 34.8%; F=41.83, 7.14; df=1,5; MSE=0.4, 0.04; P≤0.002, 0.05; 1985, 1986) populations were negatively influenced by the absence of weeds; chewing herbivores were not affected. Total prey numbers were similarly reduced (39.2%;

Figure 2,A-B.

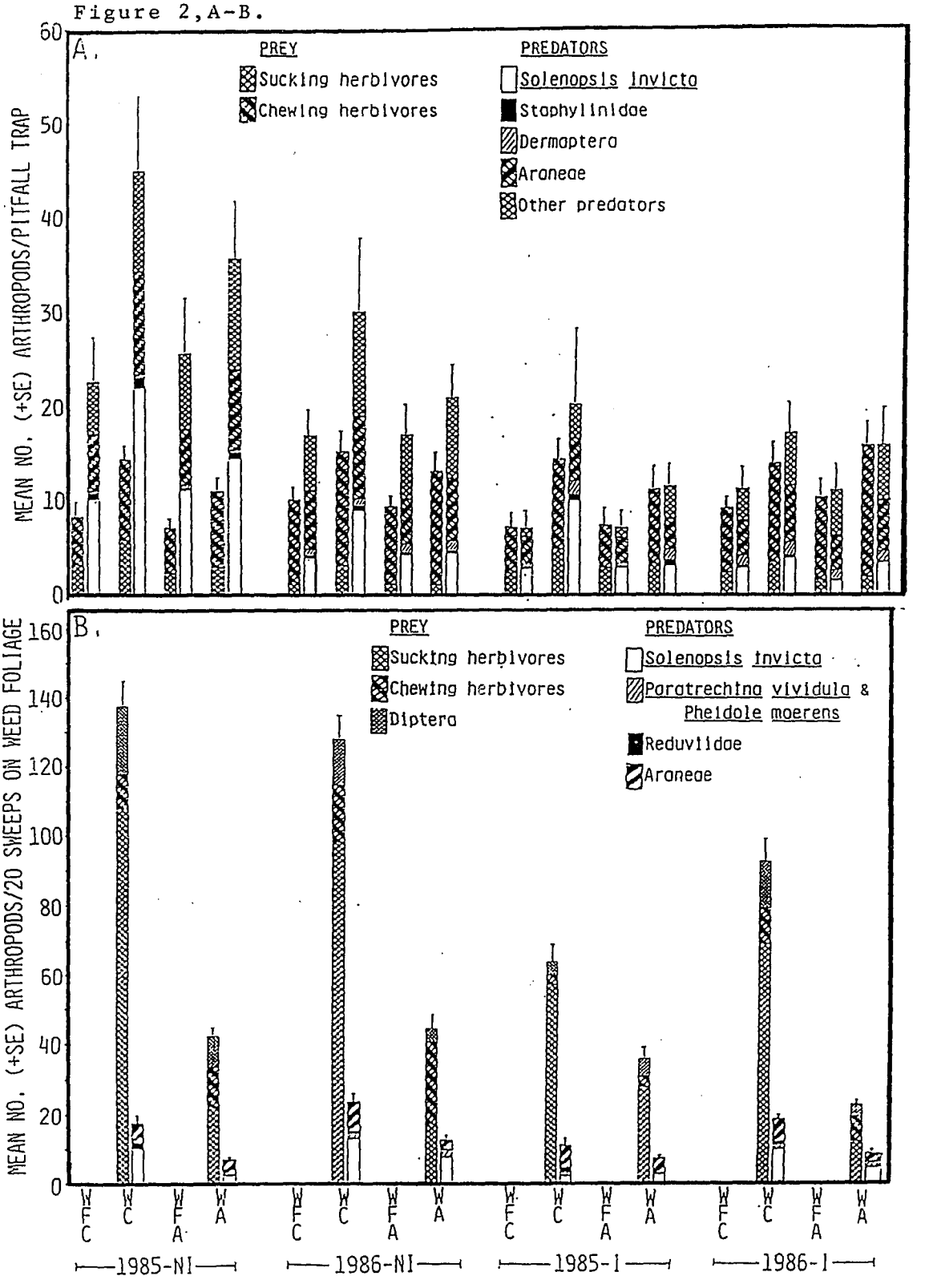
A.
PREY
Sucking herbivores
Chewing herbivores
PREDATORS
Solenopsis invicta
Staphylinidae
Dermaptera
Araneae
Other predators
MEAN NO. (+SE) ARTHROPODS/PITFALL TRAP
0
10
20
30
40
50
60
B.
PREY
Sucking herbivores
Chewing herbivores
Diptera
PREDATORS
Solenopsis invicta
Paratrechina vividula & Pheidole moerens
Reduviidae
Araneae
MEAN NO. (+SE) ARTHROPODS/20 SWEEPS ON WEED FOLIAGE
0
20
40
60
80
100
120
140
160
WFC
WC
WFA
WA
1985-NI
1986-NI
1985-I
1986-I

Figure 2,C-D.

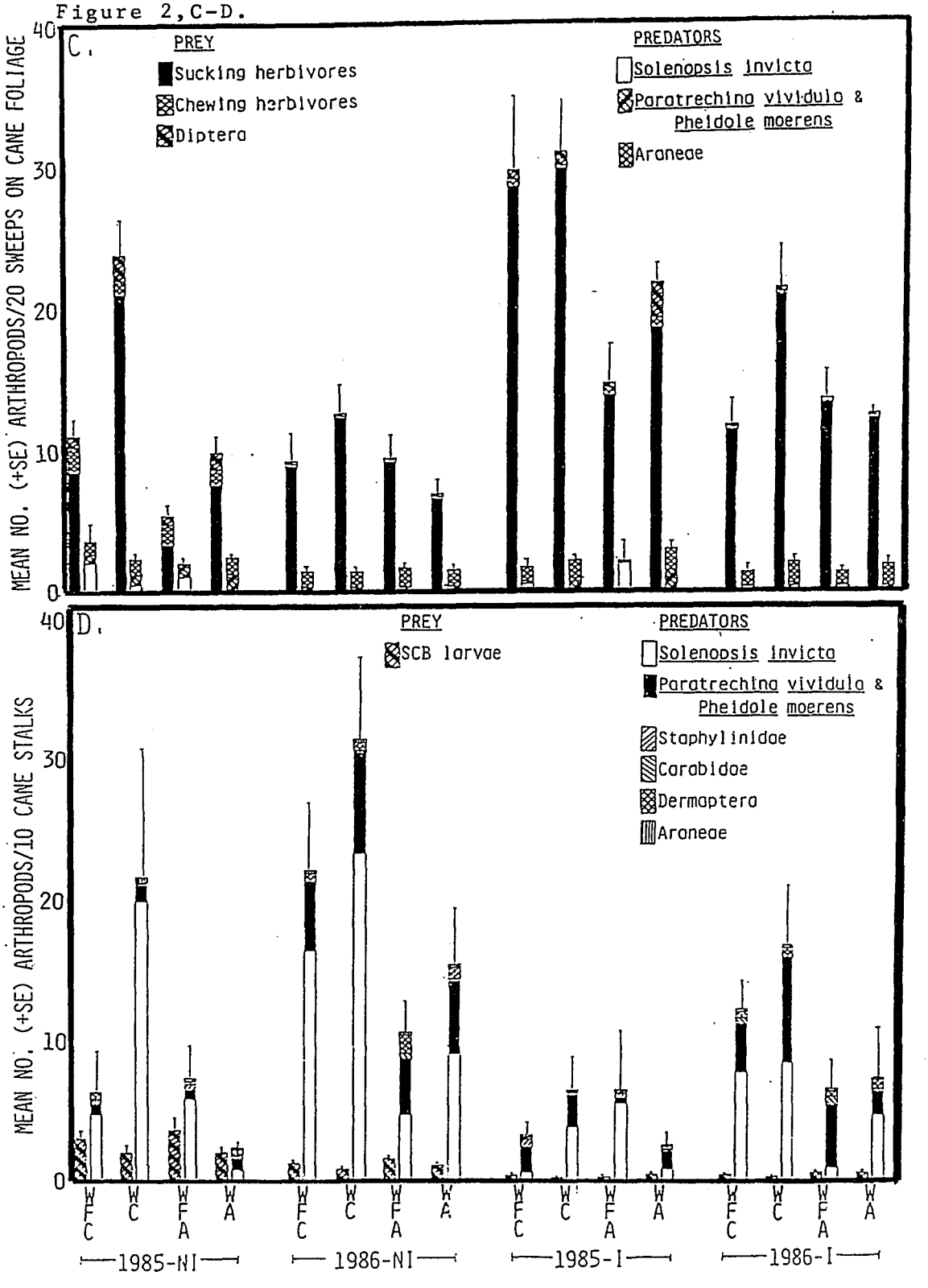
C.
PREY
Sucking herbivores
Chewing herbivores
Diptera
PREDATORS
Solenopsis invicta
Paratrechina vividula & Pheidole moerens
Araneae
MEAN NO. (+SE) ARTHROPODS/20 SWEEPS ON CANE FOLIAGE
0
10
20
30
40
D.
PREY
SCB larvae
PREDATORS
Solenopsis invicta
Paratrechina vividula & Pheidole moerens
Staphylinidae
Carabidae
Dermaptera
Araneae
MEAN NO. (+SE) ARTHROPODS/10 CANE STALKS
0
10
20
30
40
WFC
WC
WFA
WA
1985-NI
1986-NI
1985-I
1986-I

Figure 2,E.

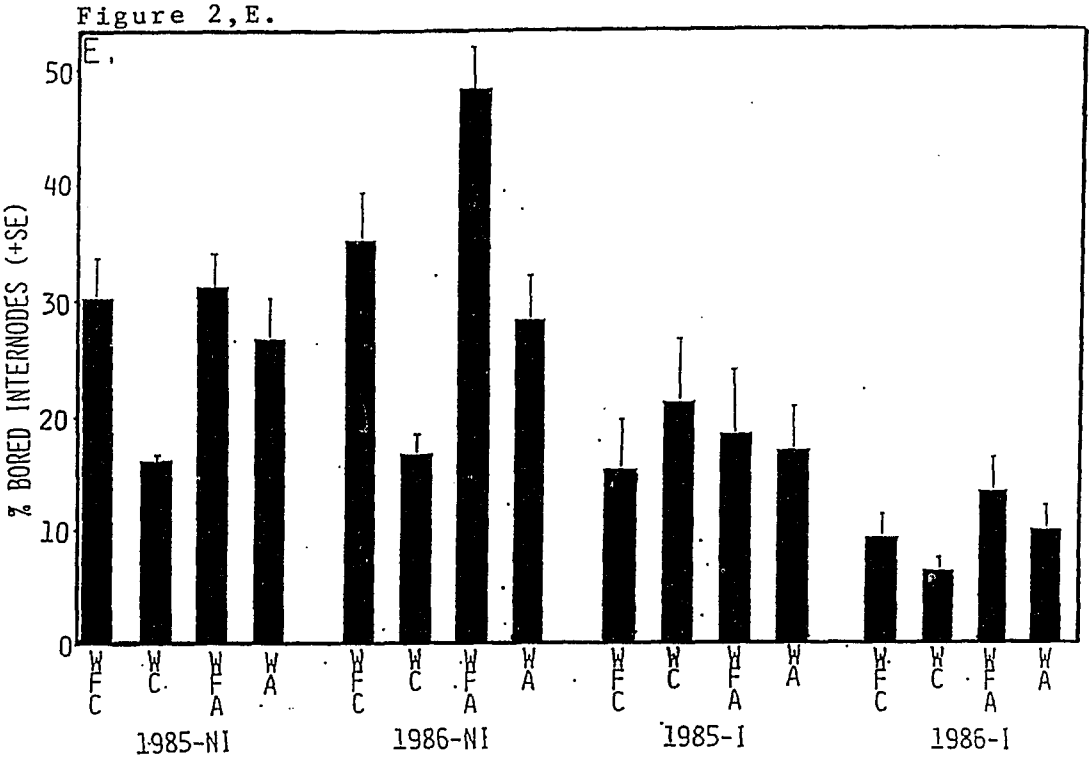

Fig. 2. Effect of weedy "W" and weed-free "WF", aldicarb-treated "A" and aldicarb-free "C", and fenvalerate-treated "I" and no insecticide "NI" treatment combinations in 1985 and 1986 on mean (+SE) numbers of selected (A) soil surface-, (B) weed-, (C) cane foliage- and (D) stalk-associated prey and predatory arthropod groups (outlined in Table 2). Sugarcane borer (SCB) damage (E) in the 8 weed, nematicide, and insecticide treatment combinations.

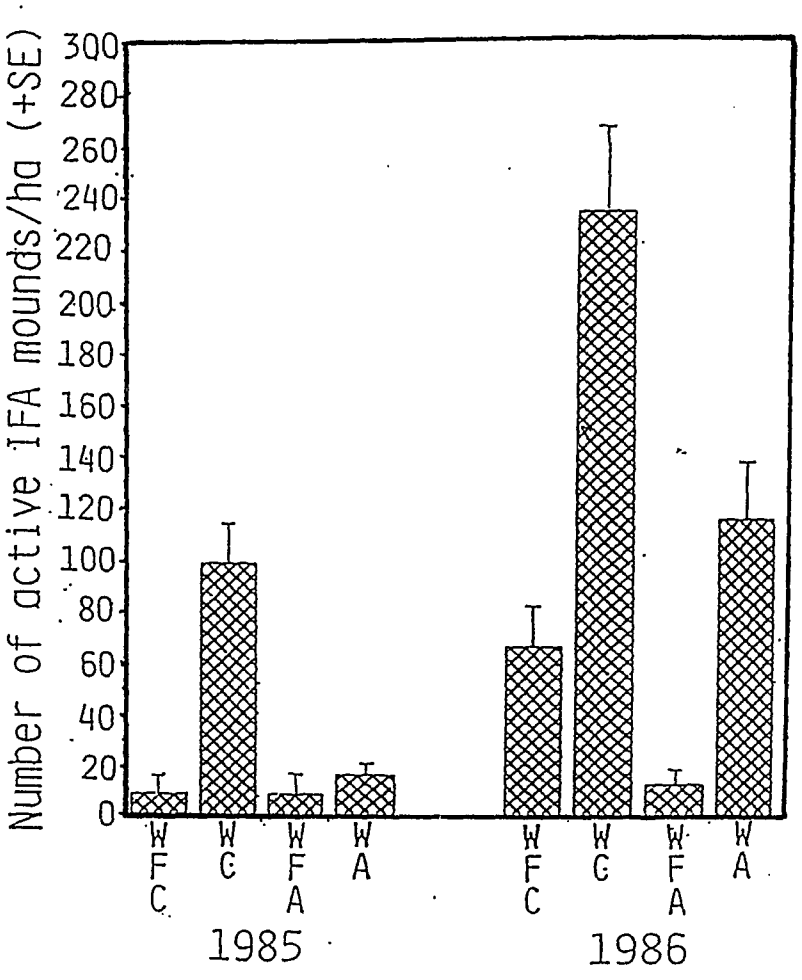

Fig. 3. Mean numbers of active imported fire ant (IFA), S. invicta, mounds per ha (+SE) in the weedy "W" or weed-free "WF", and aldicarb-treated "A" or aldicarb-free "C" treatment combinations in August, 1985 and 1986.

F=38.38; df=1,5; MSE=19.2; P≤0.002) in 1985. Total cane foliage-associated predaceous arthropod populations were not affected by weed habitat although Araneae levels were suppressed (48.1%, 42.6%; F=11.30, 8.75; df=1,5; MSE=0.4, 0.03; P≤0.02, 0.03; 1985, 1986) in WF systems and other formicids were more abundant (117.4%; F=20.2; df=1,5; MSE=0.03; P≤0.006; 1986).

Cane stalk-associated arthropods (Table 2) included few prey items with the exception of SCB larvae (Fig. 2,D). Weed growth failed to significantly alter larval SCB numbers. Even though WF habitats harbored more staphylinids in 1985 (210.1%; F=6.76; df=1,5; MSE=0.4; P≤0.05) and more carabid beetles in 1986 (183.7%; F=24.31; df=1,5; MSE=0.2; P≤0.005), total 1986 predator populations (31.1%; F=11.14; df=1,5; MSE=246.4; P≤0.02) and IFA workers (66.3%; F=16.68; df=1,10; P≤0.002) were reduced.

W cane stalks sampled at harvest incurred less SCB injury (percent bored internodes, Fig. 2,E) than the WF plants (28.1%, 42.4%; F=8.57, 57.41; df=1,5; MSE=29.1, 0.5; P≤0.05, 0.001; 1985, 1986). Table 3 shows the negative influence of weed competition on cane density (24.4%, 18.1%; F=32.65, 50.04; df=1,5; MSE=4.2, 0.5; P≤0.005, 0.005; 1985, 1986), millable cane biomass per unit area (19.0%, 15.3%; F=20.47, 20.28; df=1,5; MSE=81.3, 72.6; P≤0.01, 0.01; 1985, 1986), and tons of commercial sugar per ha (15.0%, 13.7%; F=18.40, 14.37; df=1,5; MSE=1.4, 1.2; P≤0.05, 0.05; 1985, 1986). WC-NI plots, where chemical treatments were not used, yielded 14.6 and 76.3% more net income than the WF areas, and the RIRs for the WFC-NI strategy were -1.95 and -1.98 in 1985 and 1986, respectively.

Table 3. Mean (±SE) stalk density and biomass, sucrose content, sugar yield, net dollar return, and return investment ratios of selected sugarcane ('CP 74-383') habitats at Westfield Plantation, Assumption P., LA, 1985 and 1986[a/].

Habitat[b/]	Stalks/m²		Cane yield (T/ha)[c/]		Sucrose content (% by wt of juice)		Commercial sugar (kg/ha)		Net return ($/ha)		RIR[d/]	
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
WFC-NI	14.4±0.9	7.8±0.3	144.9±8.5	66.6±3.0	16.0±0.2	16.4±0.2	16.7±1.2	8.0±0.4	1624	314	-1.95	-1.98
WC-NI	10.6±0.8	6.1±0.2	119.6±10.2	58.0±2.3	16.8±0.2	16.6±0.2	14.7±1.3	7.1±0.3	1861	554	-	-
WFA-NI	13.2±0.6	7.6±0.5	139.3±5.8	70.6±4.7	15.4±0.1	14.9±0.4	15.3±0.6	7.6±0.6	1377	30	-3.75	-4.14
WA-NI	10.1±0.9	6.6±0.4	110.8±11.8	65.1±3.8	16.2±0.2	16.0±0.4	12.9±1.4	7.6±0.6	1245	432	-27.83	-4.71
WFC-I	14.4±0.8	7.6±0.2	148.2±11.2	74.2±4.1	16.6±0.4	16.7±0.1	17.9±1.7	9.0±0.4	2297	884	4.27	3.48
WC-I	10.5±1.0	6.0±0.3	115.6±11.4	56.9±4.3	16.6±0.2	17.1±0.2	13.9±1.5	7.2±0.5	1527	674	-5.34	3.28
WFA-I	13.4±0.5	7.5±0.2	150.2±7.6	77.6±1.9	15.3±0.6	16.6±0.2	16.3±1.5	9.5±0.3	1902	874	1.26	3.07
WA-I	10.6±0.9	6.3±0.3	126.0±11.3	64.7±3.3	16.3±0.2	16.1±0.2	14.7±1.3	7.5±0.4	1768	652	-0.26	2.33

Table 3 (cont'd)

Habitat[b/]	Stalks/m^2		Cane yield (T/ha)[c/]		Sucrose content (% by wt of juice)		Commercial sugar (kg/ha)		Net return ($/ha)		RIR[d/]	
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
Contrasts[e/]												
W vs WF	0.002	0.001	0.01	0.01	0.07	NS	0.05	0.02				
C vs A	NS	NS	NS	NS	0.03	0.005	NS	NS				
I vs NI	NS	NS	NS	NS	NS	0.001	NS	0.01				

a/ 1985=plant cane crop, 1986=1st ratoon crop.

b/ W=weedy, WF=weed-free, A=aldicarb-treated, C=no aldicarb, I=fenvalerate-treated, NI=no fenvalerate.

Table 3. (cont'd)

c/ T=metric tons.

d/ RIR=return investment ratio: indicates dollar gains or losses per dollar invested in the designated pest management strategies.

e/ Values indicate level of significance for each contrast and year, NS=not significant.

Nematicide Effects. Total weed biomass was not affected by the use of aldicarb (Fig. 1). The spring aldicarb application reduced soil surface-associated haustellate herbivores (38.4%, 51.5%; F=4.30, 48.48; df=1,10; MSE=32.0, 2.5; P≦0.07, 0.0001; 1985, 1986), weed regime notwithstanding (interaction: F=12.76; df=1,10; MSE=2.5; P≦0.005; 1986), but failed to significantly diminish chewing herbivores and total prey arthropods. Although the nematicide reduced IFA colony densities (77.1%, 57.5%; F=10.64, 9.57; df=1,10; MSE=1.3, 2.8; P≦0.01, 0.01; 1985, 1986; Fig. 3) and 2nd season Araneae (18.2%; F=6.09; df=1,10; MSE=11.9; P≦0.0001) and Staphylinidae (42.9%; F=7.44; df=1,10; MSE=0.3; P≦0.02), it failed to influence the numbers of pitfall- collected IFA workers and total predators.

Weed-associated prey arthropods existed at lower levels in the A plots (65.6%, 69.5%; F=12.37, 21.11; df=1,5; MSE=2729.1, 5012.2; P≦0.05, 0.01; 1985, 1986). Sucking herbivores (74.9%, 82.5%; F=14.28, 24.07; df=1,5; MSE=2051.4, 3566.2; P≦0.05, 0.005; 1985, 1986) and dipterous prey (50.9%; F=13.57; df=1,5; MSE=78.3, 125.4; P≦0.05; 1985) were reduced by aldicarb while chewing herbivores were not significantly affected. Plant-sucking herbivores were decreased in A habitats to densities at which insecticide applications had no measurable effect (interaction: F=12.8, 3.61; df=1,58, MSE=24.0, 27.0; P≦0.001, 0.06; 1985, 1986). Total weed-associated predators were encountered in lower numbers (57.9%, 51.1%; F=7.48, 51.63; df=1,5; MSE=126.5, 58.6; P≦0.05, 0.001; 1985, 1986) where the nematicide was used; reductions were observed for IFA workers (48.0%; F=14.65; df=1,5; MSE=36.4; P≦0.01; 1986), other collective formicid species (66.8%; F=7.42; df=1,5; MSE= 0.2; P≦0.05; 1985), and Reduviidae (80.7%, 68.0%; F=6.42, 12.00; df=1,5;

MSE=2.4, 0.7; P≤0.05, 0.05; 1985, 1986).

The A habitats harbored significantly fewer cane foliage-associated sucking herbivores (56.0%, 22.7%; F=74.00, 5.31; df=1,10; MSE=30.4, 83.0; P≤0.0001, 0.05; 1985, 1986) and total prey arthropods (39.2%, 22.5%; F=65.08, 17.42; df=1,10; MSE=33.5, 85.0; P≤0.0001, 0.04; 1985, 1986). The A and WF habitats reduced sucking herbivores to low levels in contrast to the WC regime (interaction: F=10.94; df=1,10; MSE=83.0; P≤0.01; 1986). The toxic action of aldicarb against plant-sucking herbivores was observed for up to 10 weeks after each spring application. Chewing arthropod, Diptera, and predator populations were not diminished on the cane foliage by aldicarb. IFA workers, however, were less common on the A cane stalks (58.8%, 66.3%; F=3.55, 19.11; df=1,10; MSE=7.6, 0.2; P≤0.05, 0.003; 1985, 1986).

Cane in A habitats suffered more SCB damage (19.4%, 32.9%; F=4.82, 15.53; df=1,10; MSE=22.0, 0.5; P≤0.05, 0.005; 1985, 1986) and had lower sucrose concentrations (4.3%, 4.6%; F=6.56, 12.47; df=1,10; MSE=0.9, 0.6; P≤0.05, 0.005; 1985, 1986) than C cane; but aldicarb failed to significantly alter cane density, biomass per ha, and commercial sugar production per unit area. In plots where fenvalerate was not used for SCB control, the net income per ha was lower in the nematicide- and/or herbicide-treated areas. RIR values for WFA-NI and WA-NI habitats were -3.75 and -4.14 (1985), and -27.83 and -4.71 (1986), respectively (Table 3).

Fenvalerate Effects. The I plots required fenvalerate applications for SCB control on 22 June, 20 August, and 16 September, 1985, and on 10 July, 12 August, and 19 September, 1986. The insecticide did not

influence total soil surface-associated prey arthropod numbers. In contrast, fenvalerate reduced soil surface-associated IFA workers (67%, 54%; F=22.42, 5.80; df=1,20; MSE=269.0, 82.8; P≤0.0001, 0.02; 1985, 1986), other formicid species (36.4%; F=7.65; df=1,20; MSE=0.2; P≤0.006; 1986), Araneae (56.8%, 29.0%; F=55.38, 11.78; df=1,20; MSE=23.0, 20.2; P≤0.0001, 0.001; 1985, 1986), Staphylinidae (55.9%; F=0.55; df=1,20; MSE=0.4; P≤0.04; 1986), and "other" predators (75.8%, 39.8%; F=43.69, 13.29; df=1,20; MSE=67.2, 59.3; P≤0.0001, 0.0003; 1985, 1986). In 1985, however, Dermaptera populations were greater in the I plots (169%; F=9.42; df=1,20; MSE=1,7; P≤0.003) although their numbers never exceeded 1.4 per pitfall trap per 2 weeks.

The insecticide-suppressed total weed-associated prey arthropods (44.6%, 32.7%: F=9.00, 11.97; df=1,20; MSE=1102.2, 1190.2; P≤0.001, 0.001; 1985, 1986) including sucking (35.0%, 29.8%; F=8.09, 7.30; df=1,20; MSE=576.0, 729.0; P≤0.01, 0.01; 1985, 1986) and chewing herbivores (71.9%, 55.9%; F=13.29, 12.68; df=1,20; MSE=39.7, 176.9; P≤0.001, 0.001; 1985, 1986), and Diptera (68.6%; F=6.56; df=1,20; MSE=127.7; P≤0.05; 1985). The insecticide, however, failed to significantly lessen weed-associated predatory arthropod abundances.

The I habitats supported more cane foliage-associated yellow sugarcane aphids (Fig. 4), Sipha flava (Forbes), (197.2%, 63.6%; F=93.33, 18.86; df=1,20; MSE=41.0, 79.2; P≤0.0001, 0.0001; 1985, 1986), while Cicadellidae levels were lower (76.8%, 54.8%; F=18.71, 42.26; df=1,20; MSE=1.4, 0.04; P≤0.001, 0.0001; 1985, 1986) than in the NI habitats. Total prey arthropods were similarly increased (94.5%, 49.0%; F=46.90, 17.42; df=1,20; MSE=53.3, 79.2; P≤0.0001, 0.0001; 1985, 1986) including chewing herbivores (7.4%, F=17.88; df=1,20; MSE=0.8; P≤0.001)

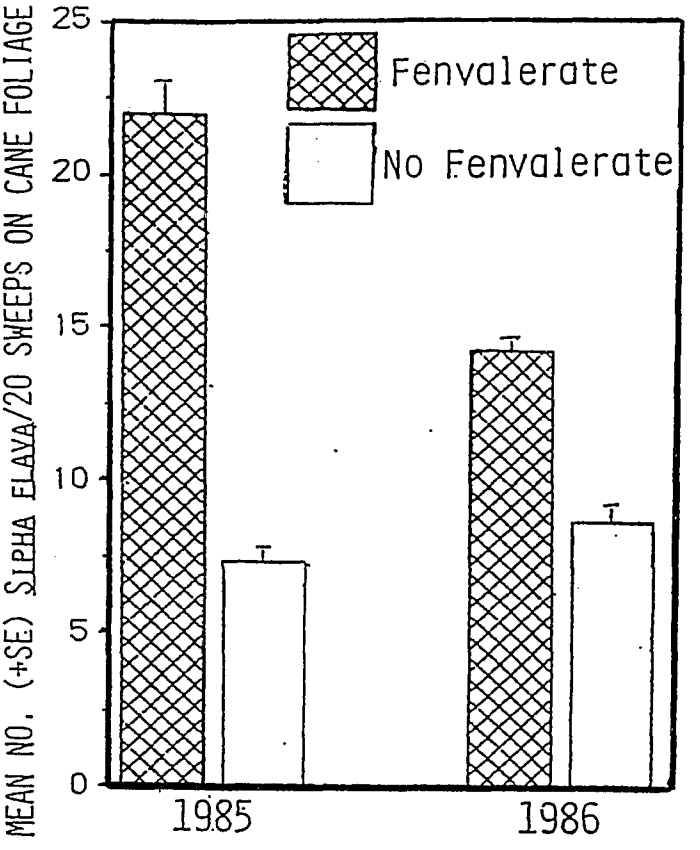

Fig. 4. The effect of fenvalerate on mean numbers of the yellow sugarcane aphid, Sipha flava (Forbes), populations collected from sugarcane leaves with a sweep net on 3 occasions in July and August of 1985 and 1986, respectively.

in 1985. Predaceous arthropods were not adversely affected by fenvalerate.

Although fenvalerate did not diminish individual predator categories (Table 2) except for Dermaptera in 1986 (38.2%; F=7.11; df=1,20; MSE=1.0; P≤0.05), total stalk-associated predatory arthropods were suppressed by the insecticide in both seasons (54.1%, 40.6%; df=1,20; MSE=357.2, 566.4; P≤0.03, 0.0001), and it effectively reduced sugarcane borer infestations in the leaf sheaths (91.8%, 68.3%; F=44.64, 29.97; df=1,20; MSE=2.6, 0.6; P≤0.0001, 0.0001; 1985, 1986) and D. saccharalis injury to the cane crop (93.1%, 70.0%; F=296.95, 198.05; df=1,20; MSE=24.0, 0.4; P≤0.0001, 0.0001; 1985, 1986) regardless of the weed- (interaction: F=11.65, 26.01; df=1,20; MSE=24.0, 0.4; P≤0.005, 0.001; 1985, 1986) and nematicide- (interaction: F=7.19; df=1,20; MSE=0.4; P≤0.05; 1986) induced effects. D. saccharalis control also resulted in higher sucrose concentrations (3.8%; F=15.48; df=1,20; MSE=0.4; P≤0.005) and commercial sugar yields per ha (8.7%; F=7.76; df=1,20; MSE=0.8; P≤0.01) by the second season. In 1986, the insecticide treatments were associated with increased cane biomass (interaction: F=4.25; df=1,20; MSE=46.2; P≤0.05) and commercial sugar production per ha (interaction: F=7.49; df=1,20; MSE=0.8; P≤0.01) primarily in the WF habitats. A 3-way interaction between the weed, aldicarb, and fenvalerate treatment factors (F=7.70; df=1,20; MSE=0.4; P≤0.05; 1986) indicated that sucrose content was most adversely affected in the WFA-NI regimes. The effective protection of the crop against the SCB resulted in overall net dollar return increases of 18.5 and 56.9% in 1985 and 1986, respectively. RIR values for I habitats were largely positive (Table 3).

DISCUSSION

Weed Effects. The diversification of weed spp. has been shown to increase beneficial arthropod fauna in several crop systems (Driggers and Pepper 1936, Altieri and Whitcomb 1980, Altieri 1981), which may result from i) attractive properties of weed extracts (Altieri 1981), ii) alternative pollen and nectar sources (Price and Waldauer 1975, Zandstra and Motooka 1978), iii) increased complexity of the chemical and physical floral mosaic that provide a greater breadth of exploitable resources (van Emden 1965, Denslow 1980, Lawton and Strong 1981), and iv) higher non-economically important prey populations that sustain more natural enemies (Allen and Smith 1958, Zandstra and Motooka 1978). In support of the latter hypothesis, we found significantly more ground-, weed-, and cane foliage-associated prey arthropods in W habitats (1985, 1986). Consequently, total ground- (1985, 1986), weed- (1985, 1986), and cane foliage- (1985), and cane stalk-associated (1986) predator densities were similarly increased. The significantly higher IFA mound densities in W systems (1985, 1986), accompanied by more intensive foraging on the ground (1985), weeds (1985, 1986), and cane stalks (1985, 1986), indicated that the key predator of the SCB (Charpentier et al. 1967, Oliver et al. 1979, Reagan 1980) was favored by the ground cover. Other formicids, P. vividula and P. moerens, collectively, were less abundant than S. invicta on the ground, weeds, and cane foliage and stalks (Fig. 3,A-D), and were not influenced by floral diversity. Although Adams et al. (1981) suggested that ant species diversity was positively correlated with predation of the SCB in Florida sugarcane, it is doubtful that P. vividula and P. moerens preyed upon SCB populations comparably to S. invicta. In fact, other formicids were not influenced

by the difference in weed regimes except on the 1986 cane foliage alone.

Araneae, however, have been recognized as the chief egg predator and second only to the IFA as an overall natural enemy of the SCB (Negm and Hensley 1969). Louisiana sugarcane fields are known to support at least 84 spider species in 18 families (Ali and Reagan 1985a), and diversity was shown to be related to vegetative complexity (Ali and Reagan 1986). Our findings indicated that spider abundances were significantly augmented on the soil surface (1985, 1986) in W habitats.

Soil surface- and cane stalk-associated earwig populations were not significantly different among the two weed regimes. Carabid and staphylinid beetles represented a small fraction of the total natural enemies collected (Table 2) and probably exerted negligible pressure on SCB populations when contrasted with S. invicta and Araneae.

The similar numbers of live SCB larvae on the cane stalks in both weed regimes suggested that the SCB did not selectively oviposit as a function of vegetative biomass or diversity. The significant reductions in percent bored cane internodes in W habitats (28.1%, 42.4%; 1985, 1986) indicated that weed growth coupled with high key predator concentrations were major factors in protection of the crop. The weed-induced declines in cane density (24%, 1985; 18%, 1986) and biomass (19%, 1985; 15%, 1986); both factors were responsible for the 15 and 14% sugar production losses observed in 1985 and 1986, respectively. In terms of RIRs, WFC-NI habitats were less desirable than WC-NI areas. Economically, the competitive impact of weeds on yield resulting from reductions in cane density was partially offset by the enhancement of natural SCB control. Because the uncontrolled weed growth competitive with the sugarcane stand, we recommend that studies be conducted on the

conservation of weeds in the furrows and early-season weed control on the cane rows only.

Aldicarb Effects. Broad spectrum pesticides have been shown to suppress predatory arthropods and to be associated with increased SCB (Charpentier et al. 1967; Negm and Hensley 1967) injury to sugarcane. Aldicarb, a systemic nematicide/insecticide for sugarcane (Birchfield 1971) reduced ground- (1985, 1986), and weed-, and cane foliage-associated total prey arthropods (1985, 1986), and appeared to be effective against sucking herbivores, weed cover notwithstanding, and Diptera. Chewing herbivores were apparently unaffected by aldicarb. As a result of the lower total prey arthropod populations, or by direct toxicity, total predaceous arthropods were reduced on the weed foliage (1985, 1986), but total predators was not suppressed on the ground, cane canopy, or cane stalks. Like the WF systems, however, A regimes had fewer IFA nests (1985, 1986). Foraging workers on the weeds and cane stalks, and ground- and weed-associated araneaids were significantly diminished in 1986.

As was observed for other chewing herbivores, live SCB larvae numbers were not reduced by aldicarb. The significantly higher levels of SCB injury in the A regimes (1985, 1986) were likely associated with the residual aldicarb-induced predator suppression. Reagan (1980) reported that natural enemies can provide 25 percent sugarcane borer control, and when predator complexes were disrupted with nonselective and persistent insecticides, SCB injury to cane increased (Charpentier et al. 1967, Negm and Hensley 1967) by as much as 69 percent (Reagan et al. 1972). The weed-nematicide interaction indicated that total

stalk-associated predator populations were at least 53.5% below those found in the WC habitats. In areas not treated with fenvalerate for SCB control, the herbicide, aldicarb, or combinations thereof appeared to be less cost-efficient than the WC habitat where chemical expenditures were minimized and floral diversity was maximized.

Fenvalerate Effects. Although fenvalerate reduced only Dermaptera and crickets, but not Araneae, Carabidae, Cicindelidae, and Staphylinidae in earlier studies (Reagan 1980), our observations indicated that fenvalerate was more lethal to ground-associated predators than herbivorous arthropods in each of the weed-nematicide treatment combinations (Fig. 2,A). Weed-associated predators, however, were not influenced by the insecticide, but the herbivores and Diptera were adversely affected. Fenvalerate was active against cane foliage-associated chewing herbivores and Cicadellidae, failed to diminish predatory arthropod levels, and significantly enhanced S. flava populations, shown in Figure 4. The specific causes responsible for the proliferation of S. flava in I sugarcane have not been determined.

Despite the diminished predator populations collected from the I plots, we found that fenvalerate was effective for SCB control when applied in accordance with Louisiana State University recommendations (Reagan 1982) regardless of the weed and nematicide regimes (Fig. 2,D,E). The significantly greater sucrose concentrations and sugar yields in the I ratoon crop suggested the importance of effective sugarcane borer control in plant cane to impede stubble decline. SCB control contributed most to the improvement of cane biomass and sugar yields in the WF habitats, where predator levels were weakest and the

potential for sugarcane borer injury was highest. Net dollar returns in I habitats were greater than in untreated areas (Table 3).

We conclude that annual weed cover supported higher predatory arthropod populations, including S. invicta, and thus helped to provide at least 28% natural protection against SCB injury. Despite the 18 and 24% (1985, 1986) declines in cane density associated with summer annual weed competition, total weed control appeared to be economically inefficient when contrasted against W-NI cane production. Aldicarb tended to reduce certain sugarcane nematode groups, including Criconemella spp., Helicotylechus spp., Paratrichodrus minor, and Pratylenchus zeae (Showler et al. 1987b), but the nematicide reduced IFA and Araneae in both weed regimes, and SCB injury to the cane increased.

Fenvalerate, although disruptive to the trophic web and associated with S. flava proliferation, was nonetheless very effective for sugarcane borer control; its use was generally more cost-effective than the insecticide-free management strategies. The use of fenvalerate was shown to compensate for the negative effects of aldicarb on sugarcane protection and for the higher SCB injury to WF cane. Due to the greater cane density and harvested biomass/ha where weeds were removed, the WFC-I habitat tended to be the most cost-efficient strategy for the maximization of commercial sugar yields and return investment ratios.

Effective integrated management of the SCB in sugarcane should discourage the use of broad-spectrum, long-residual pesticides. Weed conservation was found to be associated with high predator abundances and reduced SCB injury that partially offset the yield losses incurred through weed competition. The judicious application of an efficient and selective insecticide, however, appeared to be a profitable pest

management tactic, especially in sugarcane stands devoid of weed competition. Our study indicated that the contemporary IPM approach in Louisiana sugarcane is sound and that the diversification of native flora to enhance predatory arthropods contributed to the significant natural suppression of SCB-induced injury and associated yield losses when chemical SCB control was not used.

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CHAPTER II

AUGMENTATION AND ALDICARB-TREATMENT OF NEMATODES IN SELECTED SUGARCANE WEED HABITATS

The following chapter has been submitted to the Annals of Applied Nematology as manuscript number 87-17-1572.

INTRODUCTION

Sugarcane, an interspecific hybrid of Saccharum, is a host for at least 14 phytophagous nematode genera with Meloidogyne, Pratylenchus, Trichodorus, and Tylenchorhynchus spp. reported to be the major pests (Birchfield 1969). Aldicarb, a plant-systemic (Steele 1979) oxime carbamate with residual activity of approximately 10 weeks (Elliott et al. 1984, Showler and Reagan 1987), has been shown to improve sugarcane yields (Birchfield 1971) but failed to consistently diminish phytophagous nematode populations in several crop systems (Boag 1984, Steele 1979, Trudgill et al. 1985) including sugarcane (Waraitch 1982). Furthermore, aldicarb use has been associated with reductions of predaceous arthropods and intensified sugarcane borer, Diatraea saccharalis F., injury to Louisiana sugarcane (Showler and Reagan 1987). Recent sugarcane research has emphasized the potential contribution of annual weeds toward insect pest management (Ali and Reagan 1985, Showler and Reagan 1987) and the suppression of nematode infestations in Louisiana (Showler et al. 1987).

Host plant free amino acid (FAA) concentrations may change with biotically- and abiotically-induced stress and appear to be linked with plant resistance to herbivorous pests (White 1984), including nematodes (Lewis and McClure 1975). Sugarcane mosaic virus- and weed-induced stresses were associated with changes in sugarcane FAA accumulations; significant correlations were detected between various nematode infestations and sugarcane FAA levels (Showler et al. 1987). FAA concentrations in crop plants were demonstrated to be altered by nematode infestations (Epstein and Cohn 1971, Lewis and McClure 1975, Meon et al. 1978).

The purpose of this experiment was to examine the impacts of a systemic nematicide and augmented nematode populations on the native nematode community and FAA levels of weedy and weed-free Louisiana sugarcane. Our goal was, further, to examine the complex relationships of host plant FAA accumulations with common sugarcane stress factors.

MATERIALS AND METHODS

Experiments were conducted in a 2.5 ha test site of CP 74-383 (variety) plant (1985), then 1st ratoon (1986) sugarcane with 1.8 m row centers in Assumption Parish, Louisiana. The moisture content in the (Commerce loam; 24% clay, 68% silt, 8% sand) soil varied from saturation to occasional topsoil desiccation. The experiment was a randomized complete block design replicated 6 times with a split plot arrangement of treatments. Whole plots (0.2 ha each) were either weedy (W) or weed-free (WF). W plots were spot-treated with dicamba (9.6 g ai/l) to select for grass species as possible alternate hosts to sugarcane nematodes. In early May, WF plots were sprayed with a tank mix of metribuzin (1.3 kg ai/ha) and dicamba + 2,4-D (1.3 kg ai/ha and 2.7 l ai/ha, respectively) from a tractor-mounted spray boom. Weed quadrat samples were collected in June, August, and September of both years.

Sub plots, each 0.05 ha in area, were treated with a soil-incorporated granular formulation of aldicarb (A) (80 g ai/ha), left as untreated controls (C), or augmented with phytophagous nematodes (+). Nematodes added to the + plots were collected at the test site and raised on greenhouse Rutgers tomatoes planted in steam sterilized soil (ca. 25% sand). The nematodes proliferated on the tomatoes for ca. 5 months prior to transport to the field and were manually distributed

along the cane row tops at a rate of ca. 1200 liters per + sub plot in May of each year. Thus, at the sub plot level, six habitats were created: W+, WC, WA, WF+, WFC, and WFA.

Total weed biomass was measured by taking five random 0.5 m^2 quadrats of foliage clipped to the soil surface, two of which were partitioned by species, in June, August, and September of each year. All samples were dried for 48 h at 94° C, then weighed.

Nematodes were sampled with an Oakfield soil probe two cm in diameter to a depth of 25 cm. Two 18-core sub samples within eight cm of randomly selected cane stalks were taken from each of the six habitats in late spring, August, and October of 1985 and 1986. The 250 cm^3 soil subsamples were enclosed in plastic-lined paper bags and transported to the Mississippi State University Plant Pathology Extension Service Laboratory for nematode extraction by elutriation and sugar flotation centrifugation, and counting.

In late October 1986, the basal 10 cm of four sugarcane stalks were cut from each of the six habitat plots, sealed in plastic bags, and placed on ice. Equal quantities of cane juice were pressed from and combined within each group of four basal cane sections. A 1 ml aliquot was purified from each four-stalk juice solution using 0.45 micrometer membrane filters mounted on plastic syringes. The filtrate was stored at -100° C until FAA concentrations were measured by HPLC. All FAAs were accurately quantified except serine, which was confounded with glucosamine. SAS ANOVA procedures and correlation coefficients (SAS Institute 1979) were used to delineate relationships among the weed habitats, nematode populations, and FAA accumulations.

RESULTS

The most common nematodes collected (Appendix E) were ring, Criconemella curvata and C. onoensis (Fig. 1,A); spiral, Helicotylenchus dihystera and H. pseudorobustus (Fig. 1,B); root knot, Meloidogyne incognita and M. javanica (Fig. 1,C); stubby root, Paratrichodorus minor (Fig. 1,D); lesion, Pratylenchus zeae (Fig. 1,E); stunt, Tylenchorhynchus annulatus (Fig. 1,F); and nonphytophagous nematodes (Fig. 1,H). Lance, Hoplolaimus columbus, nematodes comprised less than 1 percent of the total phytophagous nematode populations. Because nematode populations may respond to variable soil conditions (i.e., moisture), we did not compare absolute nematode numbers across time. Due to the variation commonly encountered among nematode samples (Ferris 1984), trends are reported even when significant differences were not detected.

In 1985, the nematode inoculum (Table 1) failed to significantly increase indigenous nematode levels until October, when Meloidogyne spp., P. minor, and T. annulatus numbers were 4- (df=2,20; MSE=10493.6; $P \leq 0.03$), 3- (df=2,20; MSE=7714.7; $P \leq 0.03$), and 6-fold (df=2,20; MSE=55053.9; $P \leq 0.06$) more abundant, respectively, in the + than the C plots (Fig. 1,C,D,F). The ratoon crop Meloidogyne spp. populations in the + habitats were 8.5- (df=2,20; MSE=500.1; $P \leq 0.01$) and 5.8-fold greater than those of the C regimes in August and October, respectively. In contrast, Criconemella spp. were 42 (df=2,20; MSE=56752.1; $P \leq 0.01$) and 45% (df=2,20; MSE=163657.7; $P \leq 0.06$) lower in + plots in May and October, respectively, of 1986; Helicotylenchus spp. were similarly reduced by 80% (df=2,20; MSE=2888.3; $P \leq 0.03$), P. minor by 62% (df=2,20; MSE=779.5; $P \leq 0.01$), and total phytophagous nematodes by 40% (df=2,20;

Figure 1, A-F.

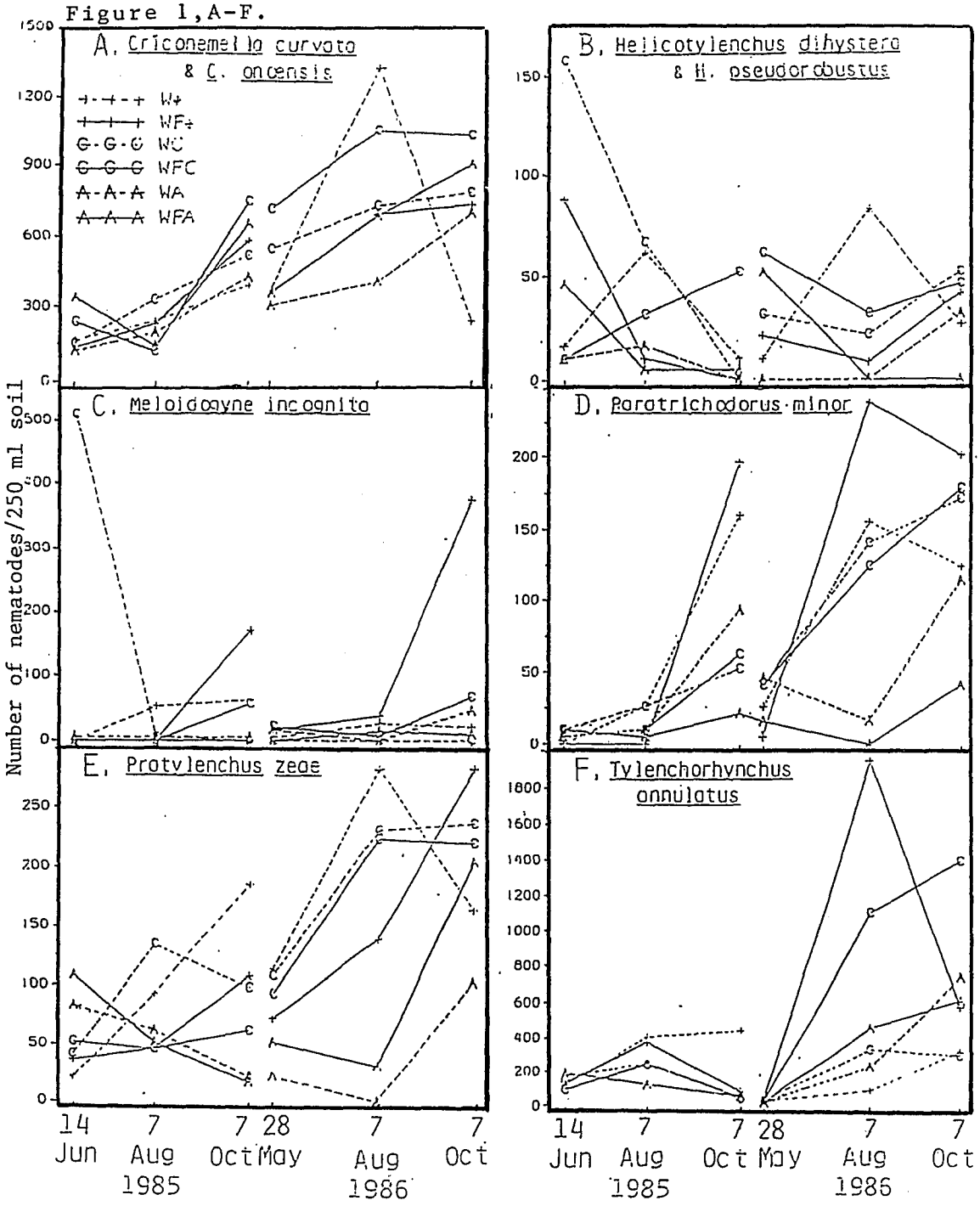
A. Criconemella curvata & C. oncensis
W+
WF+
WC
WFC
WA
WFA
B. Helicotylenchus dihystera & H. pseudorobustus
C. Meloidogyne incognita
D. Paratrichodorus minor
E. Protylenchus zeae
F. Tylenchorhynchus annulatus
Number of nematodes/250 ml soil
14 Jun
7 Aug
7 Oct
28 May
7 Aug
7 Oct
1985
1986

Figure 1, G-H.

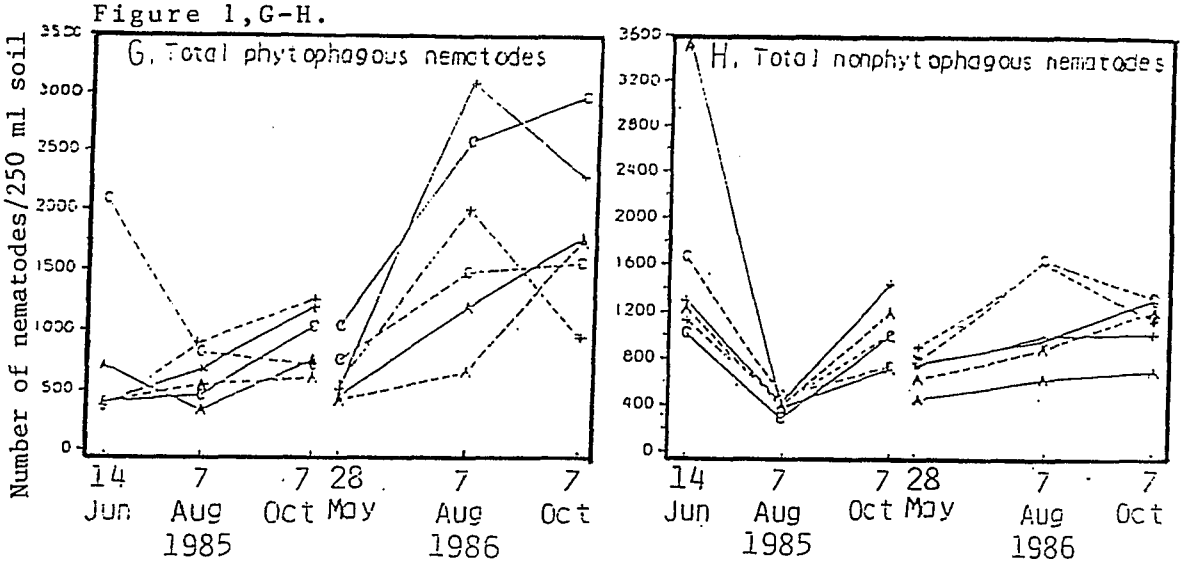

Fig. 1. Mean densities of phytophagous and nonphytophagous nematodes in weedy nematode-augmented (W+), control (WC), and aldicarb-treated (WA); and weed-free nematode-augmented (WF+), control (WFC), and aldicarb-treated (WFA) sugarcane rhizospheres in the late spring, midsummer, and fall, 1985, 1986. Figures A-H depict Criconemella spp., Helicotylenchus spp., Meloidogyne spp., Paratrichodorus minor, Pratylenchus zeae, Tylenchorhynchus annulatus, total phytophagous nematode, and total nonphytophagous nematode populations, respectively.

Table 1. Genera of greenhouse-raised phytophagous nematode[a/] inoculum levels for augmented sugarcane plots.

	Mean Number (±SE) nematodes/250 cm^3 soil						
Year	Crico-nemella	Meloid-ogyne	Para-trichodorus	Praty-lenchus	Rotyl-enchulus	Helicotyl-enchulus	Total phytophagous
1985	71±52	1080±492	44±23	159±72	10268±5347	628±137	12250±4255
1986	46±15	867±379	46±16	0	93±93	78±78	1131±441

[a/] Nematodes in greenhouse were identified to genus only.

MSE=177727.0; P≤0.05) in May 1986.

Sugarcane free cysteine was 22% lower (df=2,18; MSE=44.6; P≤0.05) where nematode populations had been supplemented; free histidine, proline, and serine were 21, 14, and 33% (df=2,18; MSE=326.6, 10716.3, 129242.3; P≤0.05) lower, respectively (Table 2). Signficant correlations were detected for the fall 1986 populations of Criconemella spp. with cysteine (r=0.47, P≤0.02, Fig. 2,A) and proline (r=0.50, P≤0.02, Fig. 2,B); Helicotylenchus spp. with glutamic acid (r=0.60, P≤0.002), and glycine (r=0.50, P≤0.02); Pratylenchus zeae with tyrosine (r=-0.53, P≤0.008); T. annulatus with arginine (r=0.47, P≤0.02), cysteine (r=0.65, P≤0.001, Fig. 2,C), histidine (r=0.44, P≤0.03), proline (r=0.50, P≤0.05, Fig. 2,D), serine (r=0.51, P≤0.01); and total phytophagous nematodes with alanine (r=0.47, P≤0.02), arginine (r=0.56, P≤0.005), asparagine (r=0.47, P≤0.03), cysteine (r=0.67, P≤0.001, Fig. 2,E), histidine (r=0.54, P≤0.006), proline (r=0.58, P≤0.003, Fig. 2,F), serine (r=0.53, P≤0.007), threonine (r=0.42, P≤0.05), tyrosine (r=-0.45, P≤0.03), and total FAAs (r=0.48, P≤0.02). The FAA concentrations that were correlated with the nematode populations followed the pattern W+≤WC≤WF+≤WFC as depicted by in Figure 2,A-F.

Compared with the C systems, aldicarb significantly reduced Helicotylenchus spp. by 79 (df=2,20; MSE=1708.4; P≤0.05) and 90% (df=2,20; MSE=453.8; P≤0.05) in August and October of 1985, respectively. P. zeae levels were similarly decreased (df=2,20; MSE=51643.5; P≤0.05) by 93% in August 1986; Criconemella spp. by 48% (df=2,20; MSE=56752.1; P≤0.05) in May 1986; P. minor by 94 (df=2,20; MSE=7987.0; P≤0.05) and 55% (df=2,20; MSE=7186.5; P≤0.05) in August and October 1986, respectively; and total phytophagous nematodes by 52

Table 2. Effects of nematode-augmented, unaltered, and aldicarb-treated weedy and weed-free habitats on sugarcane free amino acid accumulations (nanomoles per 10 µl sugarcane juice) in preharvest basal internodes, 1986.

	Treatment[a/]						Mean separations	
Free amino acid	W+	WC	WA	WF+	WFC	WFA	W vs WF[c/]	+ vs C vs A[d/]
Alanine	343.4	372.6	501.1	749.6	796.5	692.2	***	-
Arginine	160.5	138.4	142.0	216.9	306.3	316.0	***	-
Asparagine	1245.1	1236.4	1158.0	1715.0	1835.5	2265.8	***	-
Cysteine	5.2	9.3	18.9	80.6	101.4	96.5	***	b,a,a
Glutamic acid	207.1	213.8	209.2	190.8	216.3	250.4	-	-
Glycine	858.6	681.4	685.1	929.8	1042.2	1582.2	**	-
Histidine	47.0	66.1	52.0	99.9	120.2	119.2	***	b,a,ab
Isoleucine	57.0	73.8	67.4	112.1	117.5	122.7	***	-
Leucine	22.5	39.8	32.5	68.8	66.8	72.2	**	-
Lysine	11.0	12.9	14.6	26.8	26.6	33.6	**	-
Methionine	8.5	13.8	16.7	26.8	24.7	33.0	*	-

Table 2. (cont'd)

	Treatment[a/]						Mean separations	
Free amino acid	W+	WC	WA	WF+	WFC	WFA	W vs WF[c/]	+ vs C vs A[d/]
Phenylalanine	20.7	28.0	25.4	37.6	45.5	39.2	*	-
Proline	511.6	650.2	997.4	1045.2	1167.8	1196.9	***	c,b,a
Serine[b/]	642.2	763.6	596.5	890.6	1516.3	1433.9	***	b,a,ab
Threonine	80.0	77.6	74.0	141.4	156.8	188.4	***	-
Tyrosine	492.8	462.4	467.2	386.4	407.9	419.8	**	-
Valine	139.1	155.8	144.1	241.0	244.5	273.6	***	-
Total[b/]	4711.0	4996.0	5201.9	6959.3	8192.8	9135.4	***	-
Total-serine[b/]	4068.8	4232.3	4605.3	6068.7	6676.5	7701.7	***	-

a/ W+ = Weedy, nematodes added; WC = weedy, control; WA = weedy, aldicarb; WF+ = weed-free, nematodes added; WFC = weed-free, control; WFA = weed-free, aldicarb.

b/ Serine was confounded with glucosamine during HPLC analysis so results for serine and total free amino acids may not be accurate.

Table 2. (cont'd)

[c] Differences were detected using the F test; - = NS, * = P≤0.05, ** = P≤0.01, P≤0.005.

[d] Different letters indicate the significant (P≤0.05) differences detected among the means of +, C, and A nematode regimes, respectively, according to DMRT.

Figure 2,A-F.

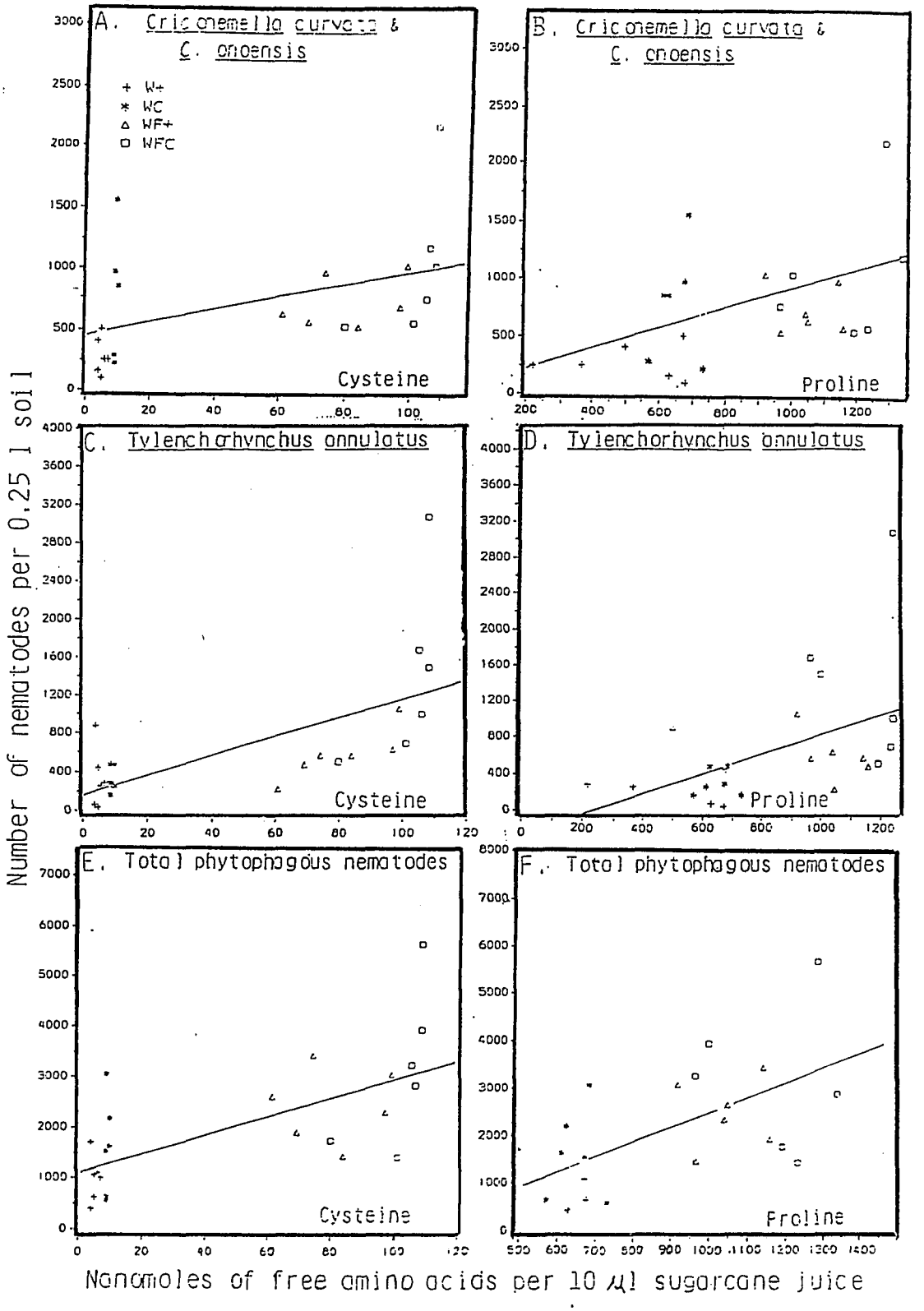
A. Criconemella curvata & C. onoensis
+ W+
* WC
Δ WF+
□ WFC
Cysteine
B. Criconemella curvata & C. onoensis
Proline
C. Tylenchorhynchus annulatus
Cysteine
D. Tylenchorhynchus annulatus
Proline
E. Total phytophagous nematodes
Cysteine
F. Total phytophagous nematodes
Proline
Number of nematodes per 0.25 l soil
Nanomoles of free amino acids per 10 µl sugarcane juice

Fig. 2. Correlations of preharvest 1986 Criconemella spp., T. annulatus, and total phytophagous nematodes in weedy nematode-augmented (W+) and control (WC), and weed-free nematode-augmented (WF+) and control (WFC) sugarcane with selected free amino acids. Figure 2, A & B show the correlation of Criconemella spp. with free cysteine ($r=0.47$, $P \leq 0.02$) and proline ($r=0.50$, $P \leq 0.02$), respectively. Figure 2, C & D depict the correlation of T. annulatus with free cysteine ($r=0.65$, $P \leq 0.001$) and proline ($r=0.50$, $P \leq 0.0.05$), respectively. Figure 2, E & F show the correlation of total phytophagous nematodes with free cysteine ($r=0.67$, $P \leq 0.001$) and proline ($r=0.58$, $P \leq 0.003$), respectively.

(df=2,20; 177727.0; P≤0.05), 50 (df=2,20; MSE=1718443.9; P≤0.05), and 67% (df=2,20; MSE=781793.4; P≤0.05) in May, August, and October 1986, respectively. Free proline was found to be 18% (df=2,18; MSE=10716.3; P≤0.05) more concentrated in aldicarb-treated cane (Table 2). The other 16 FAAs and total FAAs were not significantly altered by the nematicide. Interactions (df=2,18; P≤0.05) between the weed and nematode treatment factors were detected for arginine (MSE=2479.4), cysteine (MSE=10716.3), and proline (MSE=44.6) (Table 2).

Weeds encountered in the W habitats were Brachyaria platyphylla Nash, Digitaria sanguinalis Scop., Echinochloa spp., Cynodon dactylon Pers., Panicum dichotomiflorum Michx., and Cyperus esculentis L. Total weed biomass in each of the three nematode regimes is shown in Figure 3. As shown in Table 3, differences in the relative biomass of each weed species were not detected among the nematode regimes.

Weed growth was not associated with altered nematode populations until August of the 1st ratoon season, when T. annulatus and total plant-parasitic nematodes (Fig. 1,G) were 82 (df=1,5; MSE=241686.2; P≤0.002) and 40% (df=1,5; MSE=564741.4; P≤0.01) lower than those of the WF plots. In samples collected two months later, Criconemella spp., T. annulatus, and total phytophagous nematode populations were 31 (df=1,5; MSE=32731.5; P≤0.07), 48 (df=1,5; MSE=45987.3; P≤0.02), and 40% (df=1,5; MSE=156358.7; P≤0.04) less, respectively, in the W habitats.

Table 2 shows that, in the presence of weed competition, 16 of the 17 sugarcane FAAs were significantly (df=1,5; P≤0.05) diminished. Free alanine was lower (46%, MSE=59002.4), as was arginine (47%, MSE=830.9), asparagine (36%, MSE=87045.0), cysteine (88%, MSE=103.9), glycine (35%, MSE=95307.9), histidine (51%, MSE=169.2), isoleucine (43%, MSE=596.2),

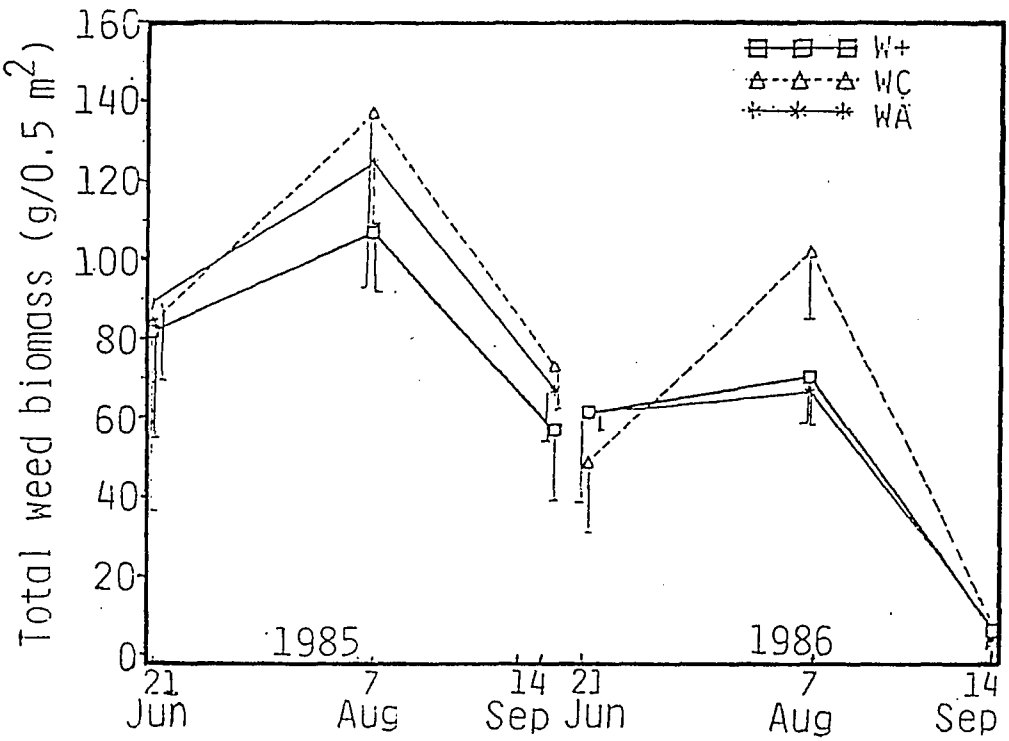

Fig. 3. Seasonal biomass (g/0.5 m^2 -SE) of annual monocot weeds in sugarcane habitats, 1985, 1986. Significant ($P \leq 0.05$) differences between weedy and weed-free regimes were detected for all sampling, but not among the weedy nematode-augmented (W+), control (WC), and aldicarb-treated (WA) habitats.

Table 3. Relative biomass of annual monocot weed species in weedy nematode-augmented (+), control (C), and aldicarb-treated (A) habitats averaged over 1985 and 1986[a/].

		Percent (MSE)[b/] of total weed biomass					
Nematode		Panicum	Brachyaria	Digitaria	Echinochloa	Cynodon	Cyperus
Regime	Month	dichotomiflorum	platyphylla	sanguinalis	spp.	dactylon	esculentis
+	June	1.8 (68.2)	5.8 (196.1)	85.4 (595.0)	2.7 (57.3)	4.2 (58.7)	0.6 (1.0)
	August	0.6 (210.1)	4.1 (140.6)	91.8 (727.1)	0.4 (13.3)	3.3 (126.6)	0.0 (3.3)
	September	2.4 (22.2)	1.0 (12.7)	83.8 (611.3)	2.3 (36.8)	9.5 (557.0)	0.0 (0)
C	June	7.2	6.2	75.9	5.6	4.6	0.4
	August	9.9	7.0	78.6	1.3	4.8	0.0
	September	0.6	1.3	64.0	4.1	14.8	0.0
A	June	7.1	4.3	80.9	2.5	5.2	0.0
	August	11.0	1.5	74.0	3.2	9.5	0.8
	September	0.4	3.8	90.6	2.8	2.5	0.0

a/ Significant ($P \leq 0.05$) differences were not detected among nematode regime means within each month. Weed biomass determined using 6 replicates of two 0.5 m^2 quadrats per 0.02 ha plot.

b/ MSEs represent variation within each month and across the nematode treatment regimes.

leucine (55%, MSE=490.6), lysine (55%, MSE=100.9), methionine (53%, MSE=105.3), phenylalanine (40%, MSE=156.5), proline (36%, MSE=25294.9), serine (47%, MSE=75686.5), threonine (51%, MSE=1174.0), tyrosine (14.6%, MSE=3018.5) valine (42%, MSE=3615.5), and total FAAs (36%, MSE=1729520.0) than in the WF cane. Asparagine was found to be the major FAA component (30.6%) of the cane juice.

Discussion

The augmentation of nematodes did not result in higher populations until nearly one full growing season had elapsed. Although all 7 observed phytophagous nematode genera were present in the greenhouse-cultured inoculum, most of the augmented nematodes were Meloidogyne incognita and M. javanica (Table 1); thus, it was not unexpected that Meloidogyne spp. populations were enhanced in the + habitats. The occasionally lower Criconemella spp., Helicotylenchus spp., P. minor, and total phytophagous nematode levels possibly resulted from interspecific competition for available root space (Barker and Olthof 1976).

The augmented nematode, especially Meloidogyne spp., infestations in the October 1986 + systems were associated with the relatively low accumulation of free cysteine, histidine, proline, and serine. The weed-nematode interaction between the six treatment combinations indicated that arginine levels were significantly higher in WFC and WFA sugarcane than the weed- and/or nematode-stressed plants. Our results suggest that Criconemella spp., Helicotylenchus spp., T. annulatus, and total phytophagous nematode levels were related to changes in specific FAA accumulations, and that free tyrosine concentrations were inversely

related to reduced Pratylenchus zeae densities. FAA concentrations may be altered by Longidorus africanus (Epstein and Cohn 1971), Meloidogyne incognita (Lewis and McClure 1975, Meon et al. 1978), Radopholus similis (Hanks and Feldman 1963), and Xiphenema spp. (Ferris 1984) in various crops. Showler et al. (1987) found that sugarcane mosaic virus- and weed stress-induced changes in free cysteine accumulations were correlated ($r=0.59$, $P \leq 0.001$) with T. annulatus populations. Lewis and McClure (1975) found that Meloidogyne-susceptible cotton had higher levels of certain FAAs, but lower total FAA accumulations, than resistant plants, but the importance of specific FAAs to selected nematode species has not been determined. Meon et al. (1978), however, found that proline, a component of Meloidogyne javanica egg shells (Bird and McClure 1976), increased with M. javanica populations in tomatoes, especially during egg production. We discovered that FAA accumulations were altered by biotic stresses and that specific FAAs may be related to population densities of selected phytophagous nematodes.

Although aldicarb has been reported to increase sugarcane yields (Birchfield 1971), it failed to provide season-long control of phytophagous nematodes in our, and in other (Waraitch 1982), sugarcane studies. Aldicarb, however, may merely impede nematode migration in the soil instead of causing mortality (Hough and Thomason 1975, Huang et al. 1983, Trett and Perry 1985). Free proline was significantly more concentrated in aldicarb-treated cane (indicated by the weed-nematode treatment factor interactions). Aldicarb has also been shown to alter the protein content of, and to induce stress upon, tobacco (Balayannis 1983) and sugarbeet plants (Varaprasad and Mathur 1980). For this reason, and due to the nematicidal effect of aldicarb, FAA

concentrations were not correlated with nematode abundances in the A regimes.

Baird and Bernard (1984) found that nematode population trends require nearly one full season to become apparent; differences between phytophagous nematode populations in the two weed regimes were not detected until mid-way through the ratoon season. Of the six phytophagous nematode groups encountered, Criconemella spp., T. annulatus and total plant-parasitic nematodes were lower in the weedy plots. Although McSorley and Campbell (1980) found that weed growth resulted in intensified Pratylenchus brachyurus and Rotylenchus reniformis densities on avocado roots, and weeds can host many injurious nematodes (Bendixon et al. 1979), other studies have indicated that certain plants, including Melilotus indica (All.), Ligustrum vulgare (L.) (Birchfield and Martin 1956), and Digitaria decumbens (Stent) (Haroon and Smart 1980) may be antagonistic to nematode populations. We suggest that the different nematode species were suited differently to the various weed species. Weed-induced competitive stress appeared to be related to changes in 16 of the 17 detected sugarcane FAAs detected. For more detailed analyses of of weed effects on sugarcane nematode and FAAs, see Showler et al. (1987).

This investigation indicated that weed- and nematode-induced stresses resulted in lower FAA concentrations, but that aldicarb, accompanied by reduced phytophagous nematode infestations, was associated with greater levels of free proline. We conclude that the stress-induced changes in FAAs were related to the abundances of three of the six observed plant-parasitic nematode groups.

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CHAPTER III

NEMATODE INTERACTIONS WITH WEEDS AND SUGARCANE MOSAIC VIRUS IN LOUISIANA SUGARCANE

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INTRODUCTION

Of the 14 plant-parasitic nematode genera reported in Louisiana soils on which sugarcane, interspecific hybrids of Saccharum, is grown, Birchfield (1969) identified Trichodorus, Tylenchorhynchus, Meloidogyne, and Pratylenchus spp. as the major pests (Birchfield 1969). Crop loss prediction models are based on initial phytophagous nematode populations (Seinhorst 1966, Seinhorst and Kozlowska 1977, Ferris et al. 1981) and neglect other factors that may impact upon nematode abundances, including tillage regimes (Caveness 1974, Thomas 1978, Fortnum and Karlen 1985, Parmelee and Alston 1986), organic soil augmentation (Solhenius 1980, Peterson and Luxton 1982), varietal resistance (Anzalone and Birchfield 1977, Niblack et al. 1986), the number of seasons a cultural practice is implemented (Baird and Bernard 1984), the size and nutritional quality of available root space (Nusbaum and Ferris 1973, Barker and Olthof 1976), fungal-nematode (Ferris et al. 1981, Huang and Chu 1984, Morgan-Jones et al. 1986, Smith et al. 1986) and nematode-nematode (Goswami et al. 1974, Duncan and Ferris 1982) interactions, insect herbivory (Noling et al. 1984), and antagonistic plant species (Birchfield and Martin 1956, Hanks and Feldman 1963, Miller and Ahrens 1969).

White (1984) indicated that host plant stress-induced changes in free amino acid (FAA) concentrations may contribute to the proliferation of phytophagous organisms by providing easily assimilated nitrogen. Host plant free proline levels, in particular, have been shown to respond to nematode (Cohn and Orion 1970, Epstein and Cohn 1971, Meon et al. 1978, Griffin 1980), bacterial (Seitz and Hochster 1964, Meon et al. 1978), and viral (Jenkins and Taylor 1967, Cooper and Selman 1974)

stresses. Lewis and McClure (1975) indicated that cotton resistance Meloidogyne incognita may be related to accumulations of specific FAAs.

Although avocado roots were shown to harbor greater nematode populations in weedy systems than weed-free areas (McSorley and Campbell 1980), the effects of weed cover on phytophagous nematodes in other agroecosystems and on crop FAAs have not been examined. Research on the contribution of annual weeds toward sugarcane borer (SCB), Diatraea saccharalis F., control (Ali et al. 1984, Showler and Reagan 1987), and water stress-induced changes in FAA accumulations in various plants (Barnett and Naylor 1966, Routley 1966, White 1984), we examined the relationship of weed competition with FAA concentrations and the nematode community structure.

Plant virus stresses also may alter the nematode (Bird 1969, Goswami et al. 1974, Taylor 1979, Huang and Chu 1984) and FAA (Doke 1972, Cooper and Selman 1974, Gildow 1980, Ajayi 1986) levels of various crop hosts. Although sugarcane mosaic virus (SCMV), a wide-spread Louisiana sugarcane disease (Koike and Yang 1971), was implicated in synergistic and additive yield loss interactions with ratoon stunting disease (Koike 1974) and Pythium graminicola (Apt and Koike 1962), respectively, the potential interrelationship of SCMV with nematode abundances and FAA accumulations in sugarcane has not been addressed.

Nematode infestations may be linked with other biotic stress agents, and the relationship is probably mediated through the plant (Wallace 1980, Noling 1987). The purpose of this study was to observe sugarcane nematode interactions with common biotic stresses and to delineate relationships associated with host plant FAA levels.

MATERIALS AND METHODS

Studies were conducted in 2.5 ha of CP 74-383 plant, then first ratoon sugarcane (1985, 1986) on 1.8 m row centers in Assumption Parish, Louisiana. The soil (Commerce loam; 24% clay, 68% silt, 8% sand) moisture content varied from saturation to occasional topsoil desiccation. The experiment was a randomized block design replicated 6 times with a 2x2 factorial arrangement of treatments. The weedy (W) and weed-free (WF) plots were each 0.2 ha in area. The four treatments were i) weeds and virus-infected cane (WV), ii) weed-free and virus-infected cane (WFV), iii) weeds and virus-free or "healthy" (WH) and iv) weed-free and virus-free or control (WFH) cane.

In early May, WF plots received a tank mix application of metribuzin (1.3 kg ai/ha) and dicamba + 2,4-D (1.3 kg ai/ha and 2.7 l ai/ha, respectively) from a tractor- mounted spray boom. Weeds in WF habitats were spot-treated with metribuzin (25.5 g ai/l) each season. W plots were spot-sprayed with dicamba (9.6 g ai/l) to select for grass species as possible alternate hosts to sugarcane nematodes. Johnsongrass, Sorghum halepense L., a very competitive perennial weed in most agroecosystems, was completely removed from all habitats using spot-sprayed asulam (2% ai) and by hand-roguing. Weed samples were collected in June, August, and September of both years. Total weed biomass was determined by taking five random 0.5 m^2 quadrats of clipped vegetation in each treatment replicate; two of the five subsamples were sorted by weed species. All samples were oven dried for 48 hours at 94°C, then weighed.

Nematodes were collected with an Oakfield soil probe 2 cm in diameter to a depth of 25 cm. Two 18-core subsamples, taken within 8 cm

of randomly selected cane stalks, were collected from the W and WF habitats in late spring, August, and October of 1985 and 1986. SCMV-infected sugarcane stools were visually located and tagged for future reference in April of each year; in October our nematode collection system was conducted at the base of SCMV-infected and SCMV-free plants, and along the row tops at least 45 cm from sugarcane stools (interstool gaps). The 250-ml soil subsamples were kept in plastic-lined paper bags and transported to the Mississippi State University Plant Pathology Extension Service Laboratory for nematode extraction by elutriation and sugar flotation centrifugation, and counting.

In late October, 1986, the basal 10 cm of four healthy and four SCMV-infected sugarcane stalks were cut from each W and WF plot, sealed in plastic bags, and placed on ice. Equal quantities of cane juice were squeezed and combined within each group of four stalks. A 1-ml aliquot was purified from every 4-stalk juice solution using 0.45 micrometer membrane filters mounted on plastic syringes. The filtrate was stored at -100°C until FAA concentrations were measured by HPLC. All FAAs were accurately quantified except serine, which was confounded with glucosamine. SAS ANOVA and correlation procedures (SAS Institute 1979) were employed to delineate relationships among the weed and nematode populations, and FAA accumulations.

RESULTS

Weeds in W plots were Brachyaria platyphylla Nash, Digitaria sanguinalis Scop., Echinochloa spp., Cynodon dactylon Pers., Panicum dichotomiflorum Michx., and Cyperus esculentis L. The relative biomass

of each weed species is shown in Table 1.

The nematodes most commonly collected (Appendix E) were ring, Criconemella curvata and C. onoensis; root knot, Meloidogyne incognita and M. javanica; stubby root, Paratrichodorus minor; lesion, Pratylenchus zeae; reniform, Rotylenchus reniformis; and stunt, Tylenchorhynchus annulatus nematodes. Lance, Hoplolaimus columbus; and spiral, Helicotylenchus dihystera and H. pseudorobustus, composed less than 1 percent of the total phytophagous nematode populations. Because nematode populations may respond to variable soil conditions (i.e., moisture) (Noling 1987), we did not compare absolute nematode abundances across time. Figure 1 shows that nematode abundances did not necessarily follow distinct temporal patterns. Due to the variability typically found among nematode samples (Ferris 1984), trends are reported even when significant differences were not detected.

Weed effects on nematode populations. Weedy cane harbored 44 and 40% more phytophagous nematodes than WF cane in June and August of 1985, respectively. Thereafter, total plant-parasitic nematodes was reduced by as much as 46% ($P \leq 0.03$) on W cane (Fig. 1,F). T. annulatus populations tended to be lower on W cane after August 1985 by as much as 79% ($P \leq 0.05$); Criconemella spp. and Meloidogyne spp. followed a similar pattern (Fig. 1). Such relatively consistent weed-related population differences were not observed for P. minor, P. zeae (Fig. 1), R. reniformis, and nonphytophagous nematodes.

To determine whether sugarcane weeds served as nematode reservoirs, soil from the interstool gaps was examined. In 1985, P. minor, T.

Table 1. Relative biomass of annual monocot weed species in weedy regimes averaged over 1985 and 1986.

	Percent of total weed biomass[a/]				
	Panicum	Brachyaria	Digitaria	Echinochloa	Cynodon
Month	dichotomiflorum	platyphylla	sanguinalis	spp.	dactylon
May	0.6	6.0	89.8	2.8	0.6
Aug	2.2	3.2	90.1	1.5	3.0
Oct	3.8	1.4	70.4	2.4	22.2

[a/] Weed biomass was determined using 6 replicates of two 0.5 m^2 quadrats per 0.02 ha plot.

Criconemella spp.
number/l soil
A.
1985
1986
MAY JUN JUL AUG SEP OCT MAY JUN JUL AUG SEP OCT
Meloidogyne spp.
number/l soil
B.
Protylenchus zeae
number/l soil
C.
Paratrichodorus minor
number/l soil
D.
Tylenchorhynchus annulatus
number/l soil
E.
Total phytophagous nematodes
number/l soil
F.

Figure 1, A-F.

Fig. 1. Mean numbers of phytophagous nematodes (-SE) in weedy and weed-free sugarcane rhizospheres in June, August, and October of 1985 and 1986. Asterisks indicate significant differences between the two weed regimes. Figure 1,A shows that Criconemella spp. populations tended to be favored in weed-free systems in the second season. Figure 1,B portrays few Meloidogyne sp. in weed-free cane, but none in weedy cane. Figures 1,C and D depict little difference among the two weed regimes for P. zeae and P. minor populations, respectively. Figure 1,E shows that T. annulatus numbers were unaffected by the presence of weeds in 1985, but by 1986 had increased in the weed-free cane. Figure 1,F depicts higher total phytophagous nematode populations in weed-free cane in the second season.

annulatus, P. zeae, and total phytophagous nematode spp. were more abundant in W gaps than in bare soil by 100 (df=1,5; MSE=2626.7; P≤0.14), 57 (df=1,5; MSE=35791.1; P≤0.13), 47, and 49%, respectively. In 1986, however, these groups were 0, 71 (df=1,5; MSE=204276.5; P≤0.1), 36, and 41% (df=1,5; MSE=502315.9; P≤0.15) lower in the W gaps than WF gaps (Fig. 2). Juvenile Meloidogyne spp. were lower (62%) only in 1986 W gaps. The Criconemella spp. were 47 and 21% more abundant in W gaps in each respective year. Nonphytophagous nematode levels in W gaps were 68 (df=1,5; MSE=44605.3; P≤0.01) and 35% (df=1,5; MSE=121600.2; P≤0.12) higher than in WF gaps in 1985 and 1986, respectively (Fig. 2). Relative abundances of the nematode groups (percent of total plant-parasitic nematodes) were not affected by the weed regimes. Criconemella, the predominant genus, composed up to 53% of the phytophagous nematodes, but R. reniformis, Meloidogyne spp., and P. minor each accounted for less than 7% in either weed regime. Relative abundances of total nonphytophagous and plant-parasitic nematodes (% of total nematodes) failed to reveal weed-related effects.

In 1985 Meloidogyne spp. was not detected in W habitats. W gap and W cane Criconemella spp., P. zeae, R. reniformis, P. minor, T. annulatus, and total phytophagous nematode populations were approximately equivalent. By 1986 Criconemella spp., P. minor, T. annulatus, and total phytophagous nematode abundances were 49 (df=1,5; MSE=86605.9; P≤0.08), 79 (df=1,5; MSE=8392.7; P≤0.05), 26, and 40% (df=1,5; MSE=221110.7; P≤0.07) greater, respectively, on W cane than in W gaps. Meloidogyne spp. was found in W gaps but not on the cane (Fig. 2). P. zeae was evenly distributed along W cane rows.

WF cane harbored 63 (df=1,5; MSE=86622.9; P≤0.05) and 70% (df=1,5;

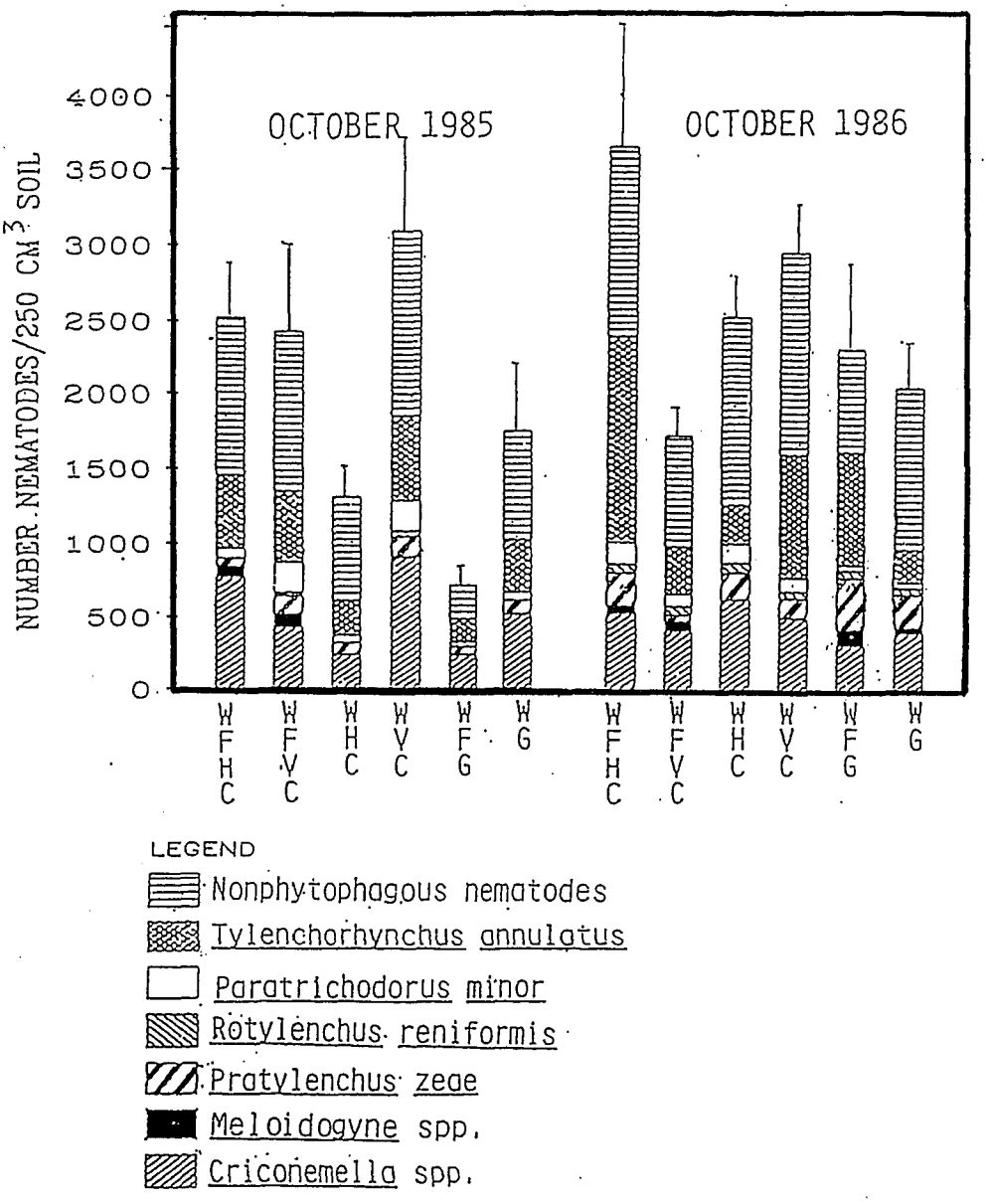

Fig. 2. Mean abundances (+SE) of phytophagous nematode species and nonphytophagous nematodes on weed-free healthy cane (WFHC), weed-free sugarcane mosaic-infected cane (WFVC), weedy healthy cane (WHC), weedy sugarcane mosaic virus-infected cane (WVC), weed-free interstool gaps (WFG), and weedy interstool gaps (WG) in a Louisiana sugarcane (CP 74-383) field in October, 1985 and 1986.

MSE=139413.1; P≤0.05) more Criconemella spp. than WF gaps, 100 (df=1,5; MSE=1537.6; P≤0.05) and 79% (df=1,5; MSE=3219.4; P≤0.01) more P. minor, 67 (df=1,5; MSE=32463.8; P≤0.05) and 46% (df=1,5; MSE=140924.5; P≤0.05) more T. annulatus, 49 (df=1,5; MSE=225464.6; P≤0.05) and 45% (df=1,5; MSE=673676.3; P≤0.05) more total phytophagous, and 76 (df=1,5; MSE=39391.0; P≤0.005) and 46% (df=1,5; MSE=130886.3; P≤0.05) more nonphytophagous nematodes in each respective year (Fig. 2). Meloidogyne spp. trends were like those observed in W plots. R. reniformis levels were consistent along the sugarcane rows.

Free alanine (MSE=43662.6), arginine (MSE=2407.6), asparagine (MSE=205529.0), cysteine (MSE=57.4), glycine (MSE=219179.8), histidine (MSE=136.3), isoleucine (MSE=236.2), leucine (MSE=143.8), lysine (MSE=57.7), methionine (MSE=41.2), phenylalanine (MSE=54.0), proline (MSE=11925.9), serine (MSE=48022.2), threonine (MSE=1099.5), valine (MSE=2218.9), and total FAAs (MSE=1687784.6) in W cane were lower than in WF cane (df=1,5; P≤0.05) as shown in Table 2. Asparagine predominated; it composed 29 and 28% of the total measurable FAAs in W and WF cane, respectively. Relative amounts of each FAA were unaffected by weed pressure, except that cysteine was 7-fold (df=1,5; MSE=0.7; P≤0.001) lower in W cane.

Interactions between weed pressure, SCMV infection, nematodes, and FAAs. Weedy and weed-free plots (0.2 ha each) harbored 1985 and 1986 natural spring SCMV infection levels of 11 and 19%, and 12 and 26%, respectively. WV cane had 44 and 55% less (df=1,5; P≤0.05) free isoleucine (MSE=410.8) and phenylalanine (MSE=66.6), respectively, than WH cane; and 65, 54, 69, 48, 50, 65, 65, 72, 73, 72, 74, 68, 64, and 41%

Table 2. Free amino acid accumulations (nanomoles per 10 µl sugarcane juice) sugarcane mosaic virus- and weed-stressed, preharvest basal internodes, 1986.

	Treatment[a/]			
Free amino acid	WFH	WFV	WH	WV
Alanine	796.5 a	414.4 b	372.6 b	276.4 b
Arginine	306.3 a	178.8 b	138.4 b	142.4 b
Asparagine	1835.5 a	1580.1 a	1236.4 b	932.1 b
Cysteine	101.4 a	43.3 b	9.3 c	93.4 a
Glutamic acid	216.3	208.8	213.8	176.3
Glycine	1042.2 a	898.5 ab	681.4 ab	541.3 b
Histidine	120.2 a	74.6 b	66.1 b	60.2 b
Isoleucine	117.5 a	88.4 b	73.8 b	41.4 c
Leucine	66.8 a	43.0 b	39.8 bc	23.1 c
Lysine	26.6 a	21.1 a	12.9 b	7.5 b
Methionine	24.7 a	24.4 a	13.8 b	6.7 c
Phenylalanine	45.5 a	28.4 b	28.0 b	12.6 c
Proline	1167.8 a	1136.0 a	650.2 b	1066.3 a
Serine[b/]	1516.3 a	1067.3 b	763.6 b	399.6 c
Threonine	156.8 a	104.5 b	77.6 bc	49.4 c
Tyrosine	407.9 bc	455.7 ab	462.4 a	404.8 c
Valine	244.5 a	198.0 ab	155.8 b	87.0 c
Total[b/]	8192.8 a	6565.5 b	4996.0 c	4390.4 c
Total-serine[b/]	6676.5 a	5498.2 b	4232.3 c	3920.9 c

[a/] Means on rows followed by different letters are significantly

Table 2 (cont'd).

($P \leq 0.05$) different according to DMRT. WFH=weed-free healthy, WFV=weed-free sugarcane mosaic-infected, WH=weedy healthy, WV=weedy sugarcane mosaic virus-infected.

[b] Serine was confounded with glucosamine during HPLC analysis so results for serine and total free amino acids may not be accurate.

less (df=1,5; P≤0.05) free alanine (MSE=22078.0), arginine (MSE=866.4), asparagine (MSE=10735.9), glycine (MSE=8642.6), histidine (MSE=96.4), isoleucine (MSE=3470.2), leucine (MSE=121.7), lysine (MSE=21.7), methionine (MSE=9.3), phenylalanine (MSE=39.1), serine (MSE=91582.2), threonine (MSE=519.7), valine (MSE=14893.2), and total FAAs (MSE=303119.1), respectively, than WFH cane. WFV cane accumulated 48, 42, 38, 25, 33, and 18% less (df=1,5; P≤0.05) free alanine (MSE=31310.7), arginine (MSE=532.2), histidine (MSE=28.0), isoleucine (MSE=334.1), threonine (MSE=640.2), and total FAAs (MSE=546565.6), respectively, than WFH cane. WV cane harbored 41, 53, 46, 64, 73, 53, 56, and 29% lower (df=1,5; P≤0.05) asparagine (MSE=47825.8), isoleucine (MSE=339.6), leucine (MSE=189.8), lysine (MSE=32.4), methionine (MSE=23.0), threonine (MSE=387.9), valine (MSE=874.0), and total FAA (MSE=729980.1) levels, respectively, than WFV stalks. FAA accumulations followed the order WFH≥WFV≥WH≥WV (Table 2). *P. zeae* densities on sugarcane were correlated with glutamic acid (r=0.52, P≤0.05) and histidine (r=0.45, P≤0.05), and *Meloidogyne* spp. numbers with total FAAs (r=0.44, P≤0.05).

A significant interaction (df=1,5; MSE=83.5; P≤0.001) between the weed and SCMV stress factors was detected for free cysteine; levels followed the scheme WFH≥WH but WFV≤WV, and WV≥WH but WFV≤WFH (Table 2). *T. annulatus* and nonphytophagous nematode numbers were correlated with free cysteine (r=0.59, P≤0.001) (Fig. 3); *Criconemella* spp. and total parasitic nematode populations followed a similar trend.

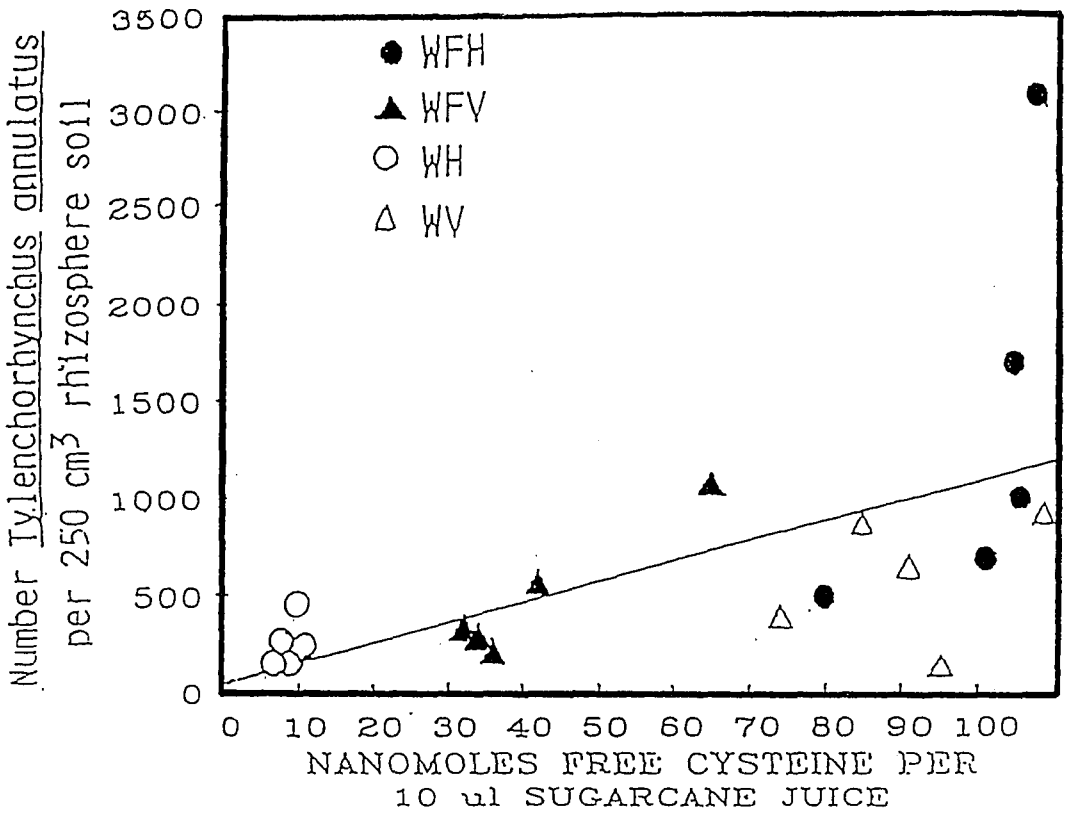

Fig. 3. Correlation of preharvest 1986 Tylenchorhynchus annulatus numbers with free cysteine accumulations in weed-free healthy (WFH), weed-free sugarcane mosaic virus-infected (WFV), weedy healthy (WH), and weedy sugarcane mosaic virus-infected (WV) sugarcane ($r=0.59$, $P \leq 0.0006$).

DISCUSSION

Weed effects on nematode populations. Criconemella spp. and nonparasitic nematodes from interstool gaps were favored by the weed cover, the weeds did not appear to act as reservoirs to the other phytophagous species. Weed effects, however, may have been partially obscured because weed biomass had declined due to cane canopy closure. Criconemella spp., P. minor, P. zeae, and total phytophagous nematode infestations on the sugarcane were greater than WF gap populations. T. annulatus levels on WF sugarcane did not exceed WF gap populations until 1986. W cane and gap populations of Criconemella spp., R. reniformis, P. minor, P. zeae, T. annulatus, and total phytophagous nematodes were not different until the ratoon season. Similarly, W sugarcane Criconemella spp., T. annulatus, Meloidogyne spp., and total phytophagous nematode population trends required nearly one season to develop; this time lag has been described by Baird and Bernard (1984).

The ratoon season crop harbored more Criconemella spp., P. minor, T. annulatus, and nonphytophagous nematodes than the W or WF gaps. W populations of P. zeae, hosted by many weed species (Manuel et al. 1980), did not differ between gaps and sugarcane but in the absence of weed growth P. zeae was more abundant in the sugarcane rhizosphere than in unvegetated gaps. Weed-induced stress appeared to be associated with the reductions of sugarcane FAAs and phytophagous nematodes.

Interactions between weed pressure, SCMV infection, nematodes, and FAAs. The weed-virus stress combinations variously affected FAA accumulations. Our results suggest that T. annulatus, Criconemella spp., and total

plant-parasitic nematode levels were related to cysteine fluctuations. Information on the role of cysteine in nematodes is sparse. Research has indicated that nematodes orient toward some root exudates (Bird 1960, Lownsbery and Viglierchio 1960, Viglierchio 1961, Bird 1962). Tomato root exudates have been shown to include glutamic acid, alanine, aspartic acid, serine, valine, phenylalanine, and cysteine, which was attractive to phytophagous nematodes in the soil (Bird 1959). Rogers (1969) found that, while some phytophagous nematodes excrete cysteine, others may retain it.

Although drought stress has been shown to increase FAA levels in plants (Barnett and Naylor 1966, Routley 1966, White 1984), the competitive effect of weeds in SCMV-free cane resulted in the reduction of FAAs and nematode populations. Virus-infected plants have been observed to harbor lesser (Goswami et al. 1974, Huang and Chu 1984) or greater (Bird 1969, Taylor 1979) nematode populations and to either reduce (Cooper and Selman 1974), increase (Ajayi 1966, Tu and Ford 1970, Lodh et al. 1971, Doke 1972), or fail to affect (Gildow 1980) FAA accumulations, and nematodes with different feeding habits affect host plant FAA levels differently (Hanks and Feldman 1963, Epstein and Cohn 1971). Nematode-induced stress may cause changes in host plant physiology to mediate its susceptibility to other pests (Noling 1987). In sugarcane, a significant weed-virus interaction was observed for free cysteine concentrations that were correlated with T. annulatus infestations. Our study emphasized that weeds, SCMV, FAA accumulations, and nematode populations were interrelated. We conclude that nematode population dynamics were influenced by factors other than initial infestation levels on the crop and involved species-dependent

interactions with common stress-related changes in host plant FAA accumulations.

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CHAPTER IV

STUDIES OF THE TERRITORIAL DYNAMICS OF THE RED IMPORTED FIRE ANT (HYMENOPTERA: FORMICIDAE) USING Zn-65 AND Mn-54

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INTRODUCTION

The imported fire ant, Solenopsis invicta Buren, indigenous to South America, is currently found in nine southeastern states (Green 1962, Lofgren 1986). Imported fire ants establish colonial (Wilson 1978, Mirenda et al. 1981) mounds with 50,000-230,000 workers (Horton et al. 1975) in pastures, cultivated areas, and woodlands (Green 1962, Lofgren et al. 1975), and forage for numerous invertebrates including springtails, leafhoppers, aphids, earthworms, and plant materials (Wilson and Oliver 1969, Ali et al. 1984).

Imported fire ants forage from tunnels that radiate from the mound 2-12 cm below the soil surface (Markin et al. 1975); this behavior implies long-term occupation of foraging areas. Territoriality, including the occupation of foraging areas by ants (Levings and Traniello 1981), has been defined as the defense of an area to monopolize its resources (Price 1975). Wilson et al. (1971) showed that S. invicta occupied discrete territories that changed seasonally. We observed S. invicta foraging areas at 24-h intervals over 23 days to study the territorial patterns associated with intercolony interactions. A rainstorm provided an opportunity to observe foraging patterns after flooding.

MATERIALS AND METHODS

Radiotracer method. Because the underground tunnels of S. invicta preclude the visual observation of territories, radiotracers were employed as markers. A colony (mound volume: ca. 9000 cm^3) was labeled with 200 µCi of Zn-65 in 19.5 ml of molasses placed in a 60-ml beaker buried flush with the soil surface, 20 cm east of the colony ("Zn

colony"). Three days later an imported fire ant colony was excavated from a nearby field, relocated 10 m south of the Zn colony to induce intercolony interaction, and similarly labeled with 200 μCi Mn-54 ("Mn colony"). Each radiotagged molasses bait was moved with its respective colony when nest relocation occurred. The radiotracers were passed through each colony by trophallaxis (Howard and Tschinkel 1981) and were detectable in ant samples within 24 h. Zinc-65 and Mn-54 have half-lives of 243.8 and 312.2 days (General Electric 1984), respectively. Therefore, since the experiment was designed to last less than 30 days, the decay correction factor was ignored.

An autogamma solid scintillation detector with a multichannel analyzer was used to distinguish and quantify the characteristic gamma radiation photopeaks of Zn-65 at 1.11 MeV (channel A) and Mn-54 at 0.83 MeV (channel B). Each sample (30 ants per bait station per day = 1 sample) was analyzed for 10 min to calculate an average count per min (cpm). Ants that had ingested Mn-54 had a cpm that exceeded background radiation counts (up to 30 cpm) registered in channel A only. Ants labeled with Zn-65 registered counts in channel B and, to a lesser extent, in channel A. Using a double-labeled dilution series of standards, cpm in channel A divided by cpm in channel B created a "channels ratio" that ranged between 0.26 and 0.29 with a mean of 0.28 (n=315). A channels ratio of over 0.29 indicated the presence of both radiolabels in the same sample and the possibility of intercolony mixing or intercolony trophallaxis.

Bait station grid. Both radiolabeled colonies were located within the Louisiana State University Radioecology Field Laboratory (McIlhenny

and Knaus 1983) amid low vegetation (Rhus radicans L., Senecio glabellus Poirot, and Sorghum halepense L.) bordered by deciduous hardwoods and shrubs. Fire ants were sampled from a total of 99 to 118 bait stations arranged in a 3 x 3 m grid (Fig. 1). At each station a 35-ml plastic cup was buried to its lip in the soil as a "receptacle cup." Identical "bait cups," their inner sides smeared with raw beef fat, were placed in the receptacle cups for 1.5 h per day to allow for foraging recruitment. Ants in the bait cups were killed with 70% ethanol and radioanalysed in the laboratory as described above. The entire procedure was repeated for 20 consecutive days, 6-25 October, 1985. Sample collection and preparation for analysis required ca. six person-hours each day; the radioanalysis procedure was automated. The foraging areas were mapped daily (Fig. 1,a-r) so that the sampling grid could be modified to include unexpected territorial changes.

RESULTS

Our method allowed the daily observation of territorial changes for 20 consecutive days. The radiotracer technique provided a precise way to indicate the presence of five classes of S. invicta: Zn-65-labeled, Mn-54-labeled, double-labeled, unlabeled ants, and no ants present. No bait cup- collected ant sample contained both radiotracers, even though the two territories abutted one another for 16 days (n=67 bait station samples). On day 18 Mn-labeled ants foraged within the previously established Zn colony's territory (Fig. 1,o).

Assuming workers foraged the 2.25 m^2 around each occupied bait station, the Zn colony used an average area (±SD) of 19.3±5.7 m^2 that ranged from 14-29 m^2, and foraged an average maximum distance of

Figure 1, a-f.

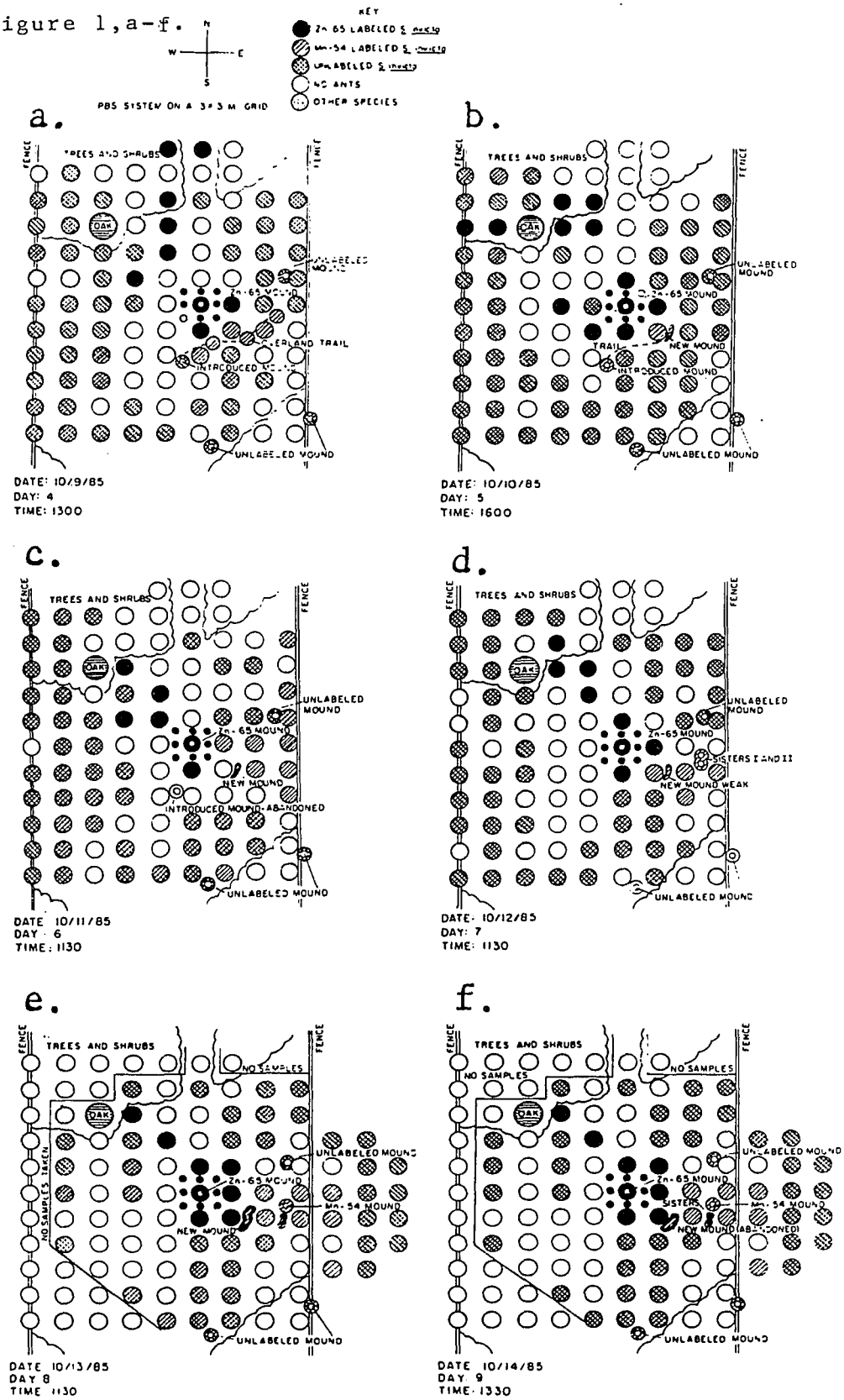
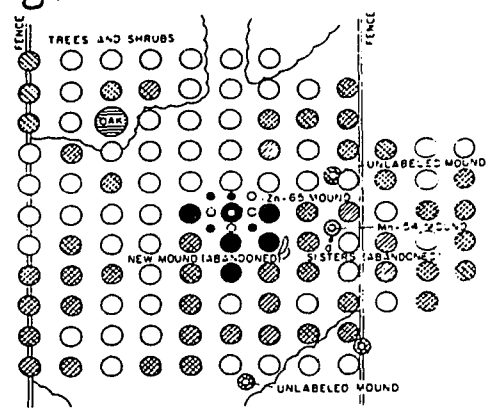

KEY
Zn-65 LABELED
Mn-54 LABELED
UNLABELED
NO ANTS
OTHER SPECIES
N
W
E
S
PBS SYSTEM ON A 3 x 3 M GRID
a.
TREES AND SHRUBS
FENCE
OAK
Zn-65 MOUND
INTRODUCED MOUND
UNLABELED MOUND
DATE: 10/9/85
DAY: 4
TIME: 1300
b.
TREES AND SHRUBS
FENCE
OAK
UNLABELED MOUND
Zn-65 MOUND
TRAIL
NEW MOUND
INTRODUCED MOUND
UNLABELED MOUND
DATE: 10/10/85
DAY: 5
TIME: 1600
c.
TREES AND SHRUBS
FENCE
OAK
UNLABELED MOUND
Zn-65 MOUND
NEW MOUND
INTRODUCED MOUND-ABANDONED
UNLABELED MOUND
DATE 10/11/85
DAY 6
TIME: 1130
d.
TREES AND SHRUBS
FENCE
OAK
UNLABELED MOUND
Zn-65 MOUND
SISTERS I AND II
NEW MOUND WEAK
UNLABELED MOUND
DATE: 10/12/85
DAY: 7
TIME: 1130
e.
TREES AND SHRUBS
NO SAMPLES
FENCE
OAK
NO SAMPLES TAKEN
UNLABELED MOUND
Zn-65 MOUND
Mn-54 MOUND
NEW MOUND
UNLABELED MOUND
DATE 10/13/85
DAY 8
TIME 1130
f.
TREES AND SHRUBS
NO SAMPLES
NO SAMPLES
FENCE
OAK
UNLABELED MOUND
Zn-65 MOUND
SISTERS
Mn-54 MOUND
NEW MOUND (ABANDONED)
UNLABELED MOUND
DATE 10/14/85
DAY 9
TIME 1330

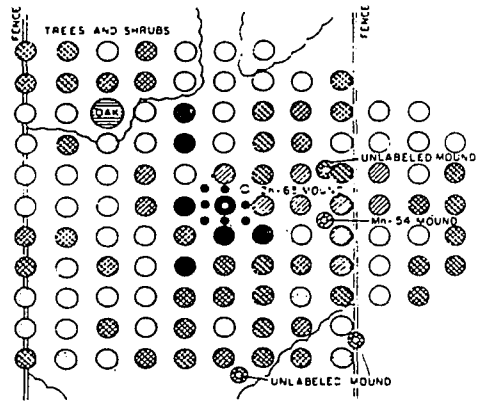
Figure 1,g-l.

g.



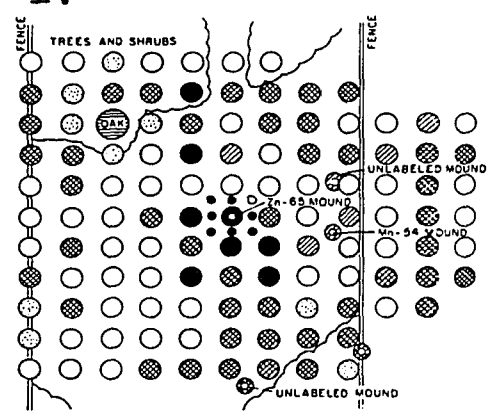
DATE: 10/15/85
DAY: 10
TIME: 1130

h.



DATE 10/16/85
DAY 11
TIME 1200

i.

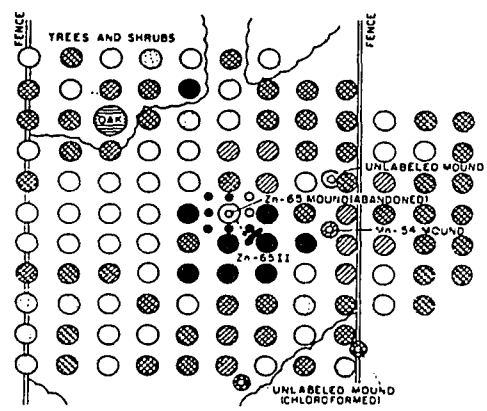


DATE: 10/17/85
DAY: 12
TIME: 1100

j.

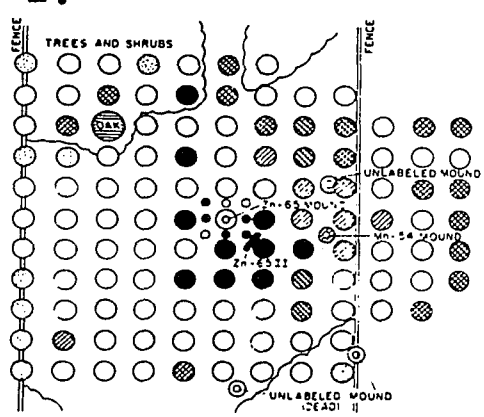
DATE: 10/18/85
DAY: 13
TIME: 1250

k.



DATE 10/19/85
DAY 14
TIME 1100

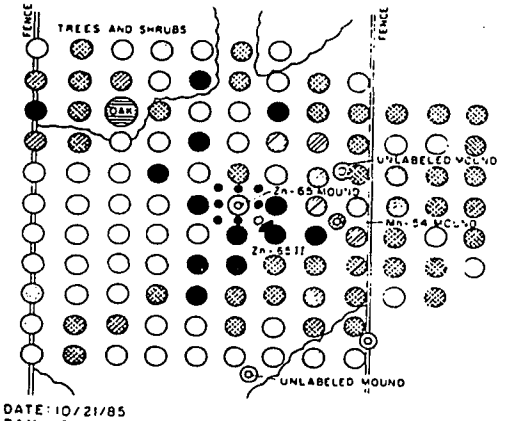
l.



DATE: 10/20/85
DAY: 15
TIME 1130

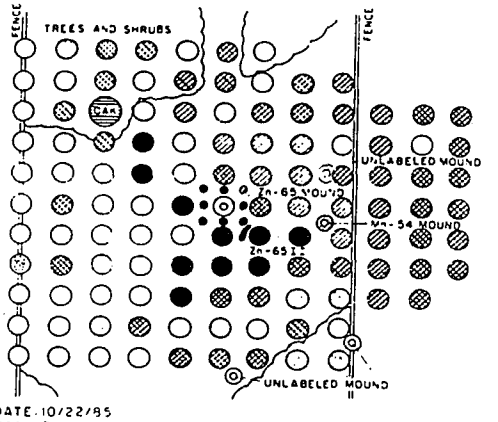
Figure 1,m-r.

m.



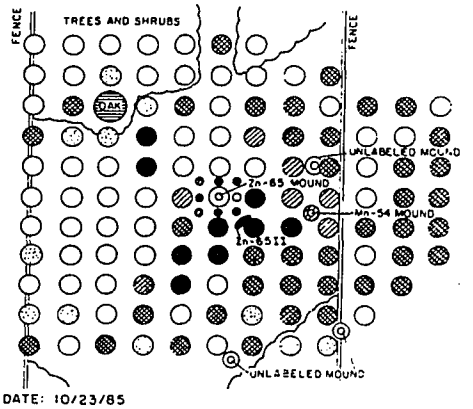
DATE: 10/21/85
DAY: 16
TIME: 1200

n.



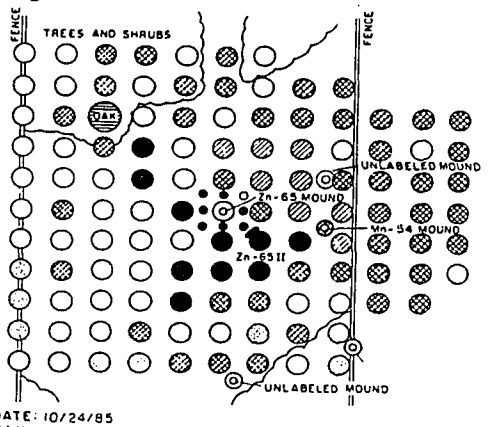
DATE: 10/22/85
DAY: 17
TIME: 1430

o.



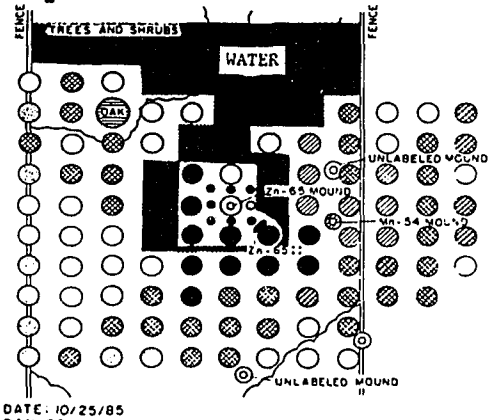
DATE: 10/23/85
DAY: 18
TIME 1430

p.



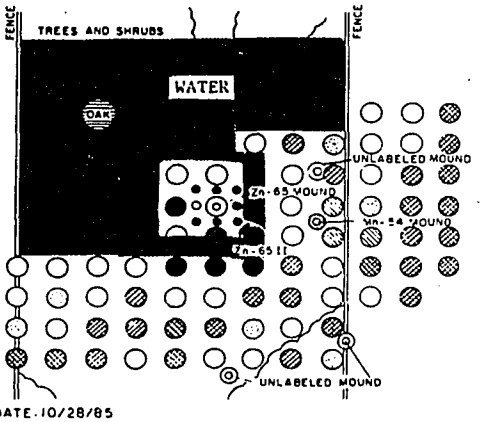
DATE: 10/24/85
DAY: 19
TIME: 1130

q.



DATE: 10/25/85
DAY: 20
TIME: 1130

r.



DATE: 10/28/85
DAY: 23
TIME: 1200

Fig. 1, a-q. S. invicta foraging areas, sampled daily for 20 consecutive days and on a 23rd day (three days after day 20 (Fig. 1,r) are shown on the bait station grid. Figures 1,a-e show the events that followed the forced introduction of the Mn colony to the study area including the fan-shaped territorial pattern that preceded mound relocation. Figures 1,e-f show that Zn-labeled ants scavenged a nest that was abandoned by the the Mn colony. Figure 1,h depicts the Mn colony foraging area as it surrounded an unlabeled nest on three sides; the unlabeled mound was then occupied (Fig. 1,i) and abandoned (Fig. 1,j) by the Zn colony. Figures 1,q-r indicate the failure of a standing water barrier to alter the foraging range of the Zn colony.

13.3±3.2 m from the mound (n=21); the greatest recorded distance was 18.5 m. After the Mn colony had formed a mound on day 8 (Fig. 1,e), it foraged an average 15.8±3.8 m^2 ranging from 7-20 m^2, and Mn-labeled workers were found to travel an average maximum distance of 11.2±1.7 m from the mound (n=13); the greatest recorded distance was 12.9 m.

The territories of the radiotagged colonies changed daily but were confined to certain sectors of the sampling grid; Figure 1,a-p shows that the Zn colony foraged consistently in the north and northwest quarter. Two days after having constructed a permanent mound (day 8, Fig. 1,e), the Mn colony foraged consistently to the northwest (Fig. 1,g-q).

The day after the Mn colony was introduced (day 4), Mn-labeled ants were found moving along a surface trail that extended 9 m northeast of the Mn-mound, and in bait stations enroute (Fig. 1,a). On day 5 the Mn colony had formed a new mound (100x15 cm basally, 2 cm in height) 6 m northeast of the introduced mound and 4.8 m southeast of the Zn colony (Fig. 1,b). Then the colony projected its territory in a fan-like shape to the northeast (Fig. 1,c). On day 7, two small "sister" mounds had been erected 5 m to the east, within the previous day's fan-like territorial extension and the "new" mound was nearly abandoned (Fig. 1,d). By day 8, a dome-shaped mound (6000 cm^3 in volume) was formed 10 cm east of the sister mounds (Fig. 1,e); it housed the Mn colony for the rest of the study (12 days). The fan-shaped territorial pattern similarly preceded a relocation of the Zn colony relocation to a site 4 m southeast of its original position (Fig. 1,j-k). During this time the Zn colony did not relinquish its former foraging area in the northwest quarter (Fig. 1,k-p). The Zn colony moved back into the original mound

after one month, where it remained for at least six more months (the tracer was still detectable in the ants).

After the Mn colony moved from the sister mounds Zn-labeled workers, not collected in bait stations, were found for two days to be carrying dead Mn-labeled ants left behind (Fig. 1,e-f), which constituted the only instances of radioisotopic mixing over 21 total days of sampling.

On day 11 the Mn colony occupied the bait stations on three sides surrounding an unlabeled S. invicta colony 4.5 m to the north (Fig. 1,h). By day 12, Mn-tagged ants were found on and within the unlabeled mound (Fig. 1,i). On day 13, the unlabeled mound was abandoned (Fig. 1,j).

Heavy rainfall the night prior to day 20 resulted in the formation of a moat of standing water 1.5-4.0 cm deep that surrounded the Zn colony (Fig. 1,q-r). Despite the water barrier, the Zn colony foraging area was not changed even after 3 days of flooding (Fig. 1,r). Ants passed to and from bait stations located across the moat through tunnel openings.

The bait station system attracted eight other Formicid species and their pattern of occurrence was also recorded (Fig. 1,h-r). Solenopsis molesta Say, Pheidole moerens Wheeler, Monomorium minimum Buckley, Paratrechina vividula Nylander, and Aphaenogaster rudis Emery were common, while 1-2 individuals of Hypoponera opaciceps Mayr, Myrmecina americana Emery, and Crematogaster clara Mayr were collected each, at a single bait station. P. vividula and S. molesta were the only two ants found in the same bait cup with S. invicta; but as S. invicta numbers increased P. vividula and P. moerens abandoned the cup to S. invicta.

DISCUSSION

The technique was useful for the delineation of changing S. invicta foraging areas and the unequivocal detection of radioisotopic combinations. The long half-lives of the radiotracers allowed detection for at least six months. The method can be useful for interpreting the effects of physical and biotic environmental factors on foraging area patterns. Holldobler (1976) suggested that ant territories include areas immediate to the nest and foraging trails, which may often shift. Although Wilson et al. (1971) observed S. invicta intercolony fighting, six discrete foraging areas that changed seasonally, and short-term territorial shifts along the edge of one foraging area, our study provided information on two entire, adjacent foraging areas on 21 days over 23 days. Forced introduction of the Mn colony allowed us to observe the subsequent complex of events as depicted by changing foraging territories.

The fan-shaped foraging pattern indicated that area-intensive scouting may precede nest relocation. Although colonies can occupy the same mound for 36 months, few stay at a particular site for more than a year (Hays et al. 1982). Colonies have been shown to move from 1 to 30 m, perhaps in response to competition for food (Green 1962). The Zn colony, however, made a 4-m move, retained its NW foraging area (apparently by using the same tunnel system), and then moved back to the original mound after three months. In South America, 20 to 25% of the S. invicta colonies examined (Jouvenaz et al. 1977) were found to host pathogens (Allen and Silvera-Guido 1974, Jouvenaz et al. 1980), unlike the nearly disease-free conditions in North America (Jouvenaz et al. 1977). Herzog et al. (1976) indicated that the chemical properties of

active S. invicta mound soil changes with time. We suggest that research be conducted on the possible association of chemical mound soil changes with the occurrence of S. invicta pathogens in South America; short-term nest relocation, triggered by specific changes in mound soil, may be a disease avoidance strategy retained by the North American populations.

Our study, in addition, indicates that S. invicta tunnel networks and territories were not disrupted by temporarily flooded soil conditions. The ability to forage unhindered by standing water appears to be partially responsible for the successful colonization of S. invicta in southeastern Louisiana.

Although the imported fire ant has been reported to compete with other ant fauna (Showler and Reagan 1987) in the U.S., our study indicates that native Formicid species were not entirely excluded from the bait station matrix and interspecific competition among ants could be further studied using modifications of our methods.

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CHAPTER V

FORAGING TERRITORIES OF THE IMPORTED FIRE ANT, *Solenopsis invicta* Buren, IN WEEDY AND WEED-FREE SUGARCANE HABITATS AS DETERMINED BY INSTRUMENTAL NEUTRON ACTIVATION ANALYSIS

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INTRODUCTION

The imported fire ant, Solenopsis invicta Buren, has colonized nine southeastern states of the U.S. (Green, 1962; Lofgren, 1986) since being introduced to Alabama from South America in 1929 (Lofgren, 1986). The worker caste forages by following trail pheromones (Wilson, 1959; Vander Meer, 1986) through subterranean tunnels that radiate from the nest mound 2-12 cm below the soil surface (Markin et al., 1975). Wilson et al. (1971) used various dye markers that were ingested by six different S. invicta colonies to demonstrate the territorial behavior of S. invicta and the effect of season on the size of foraging areas. Two adjacent fire ant colonies, fed on radiolabeled bait and studied by Showler et al. (1987a), showed delineated territorial shifts at 24 h intervals for 20 consecutive days. Foraging area patterns appeared to be associated with specific colony activities, including nest relocation.

S. invicta has been identified as an important predator of many agricultural pests (Snodgrass 1976, Sterling 1979, Reagan, 1986) including the sugarcane borer, Diatraea saccharalis (F.), in Louisiana sugarcane (Negm and Hensley 1967, Reagan et al. 1972). Recent research has demonstrated that summer annual weed cover harbored increased sugarcane borer natural enemies, including S. invicta (Ali et al. 1984, Showler and Reagan 1987a). Where insecticides were not applied, sugarcane borer injury to weedy sugarcane was found to be significantly reduced in contrast to weed-free areas (Showler and Reagan 1987a).

Instrumental neutron activation analysis (INAA) (Wang et al. 1975, Knaus and Curry 1979) provides an alternative to the applications of potentially hazardous radiotracers to the environment (Jenkins 1963),

and especially in consumable crops, often without the sacrifice of radiotracer sensitivity (Wang et al. 1975). At present, however, INAA has received scant attention in entomology. Curtis et al. (1973) successfully tagged the tsetse fly, Glossina morsitans Westwood, with ingested europium, dysprosium, gold, and iridium, and other studies indicate that dysprosium was a useful marker for Drosophila spp. dispersal (Richardson 1968).

The objective of this experiment was to evaluate the effect of weed-associated prey density on the foraging areas of discrete fire ant colonies to quantify the potential of natural predation by S. invicta in a sugarcane pest management scheme. Another goal of this study was to demonstrate the utility of INAA techniques as marking tools in the field of applied agricultural entomology.

MATERIALS AND METHODS

Studies were conducted in 2.5 ha of CP 74-383 1st ratoon sugarcane on 1.8 m row centers in Assumption Parish, Louisiana, 1986. The experiment had three weedy (W) and three weed-free (WF) areas (0.1 ha each). WF areas received an early May tank-mix application of metribuzin (1.3 kg ai/ha) and dicamba + 2,4-D (1.3 kg ai/ha and 2.7 liters ai/ha, respectively) from a tractor-mounted spray boom. Weed seedlings were spot-treated (spray was applied directly to the plants where they were found) once with metribuzin (25.5 g ai/liter) in June. The W habitats were spot-sprayed in May with dicamba (9.6 g ai/liter) to select for a dense stand of mixed grass species for another study on nematodes (Showler et al. 1987c). Johnsongrass, Sorghum halepense L., a detrimental weed inmost agroecosystems, was removed from both habitats

by hand roguing and spot-spraying with asulam (2% ai). Weed canopy growth was collected in early August by clipping five random 0.5 m^2 quadrats of foliage at six locations per habitat. Two of the five subsamples were segregated by species and all samples were oven dried at 94°C for 48 h, then weighed.

In all of the W and WF locations designated for sampling, sugarcane-associated prey arthropods were collected in four pitfall traps (Greenslade 1964), set for two weeks, then removed on August 5. Sweep nets were used to collect arthropods (Rudd and Jensen 1977) from the weed canopy with 20 sweeps per four subsamples. Sugarcane stalk-associated S. invicta foragers were sampled by examining 40 stalks (Ali and Reagan 1985) in each of six W habitat sampling locations on July 29.

Samarium (Sm), a nonradioactive rare earth element, was made available to each of three W and three WF fire ant colony mounds (ca. 400 cm^2 basally X 15 cm in height) on July 27 as 0.98 g of samarium nitrate (pH=7) mixed with 10 cm^3 of raw ground beef. The foraging area of each S. invicta colony was delineated using a bait station grid (Showler et al. 1987a) composed of a 3.65 X 3.65 m grid with 62 stations arranged on every other sugarcane row as depicted in Figure 1,A-D & F. Figure 1,E represents a grid that was abbreviated to 42 stations. Ant samples were collected in each treatment replicate (and from the fire ant mounds themselves) from July 28 to 30 from 9:00 a.m. until noon each day. One group of six S. invicta workers was removed from each sampling station per day and sealed in a labeled 2/27-dram (1 ml) plastic polyvial. Six such small vials were then sealed in a larger 2-dram (7 ml) polyvial. The samples were shipped to the Texas A&M Nuclear Science

Figure 1, A-D.

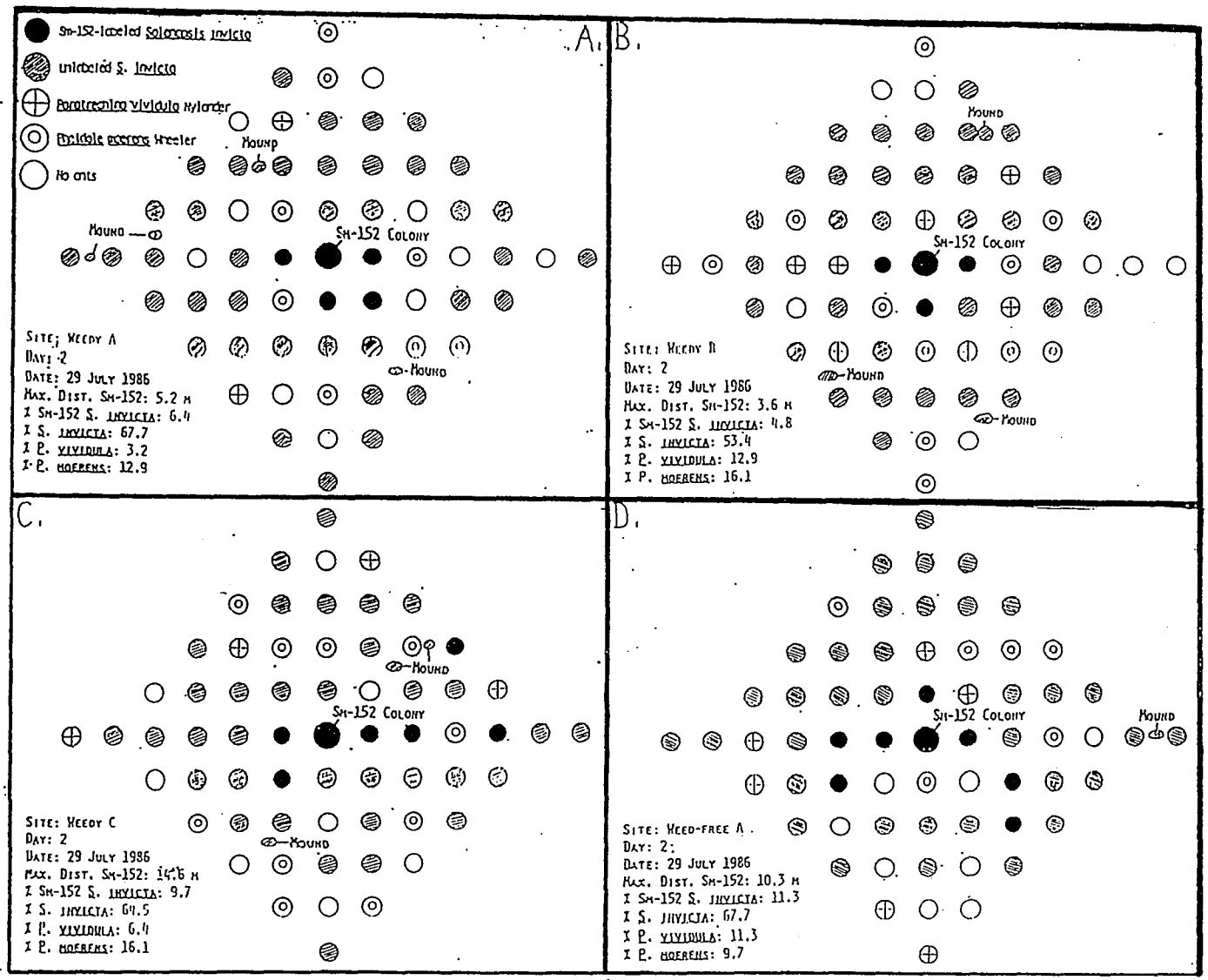
Sm-152-labeled Solenopsis invicta
unlabeled S. invicta
Paratrechina vividula Nylander
Brachymyrmex depilis Wheeler
No ants
A.
Mound
Sm-152 Colony
Site: Weedy A
Day: 2
Date: 29 July 1986
Max. Dist. Sm-152: 5.2 m
% Sm-152 S. invicta: 6.4
% S. invicta: 67.7
% P. vividula: 3.2
% P. hoffeens: 12.9
B.
Mound
Sm-152 Colony
Site: Weedy B
Day: 2
Date: 29 July 1986
Max. Dist. Sm-152: 3.6 m
% Sm-152 S. invicta: 4.8
% S. invicta: 53.4
% P. vividula: 12.9
% P. hoffeens: 16.1
C.
Mound
Sm-152 Colony
Site: Weedy C
Day: 2
Date: 29 July 1986
Max. Dist. Sm-152: 14.6 m
% Sm-152 S. invicta: 9.7
% S. invicta: 64.5
% P. vividula: 6.4
% P. hoffeens: 16.1
D.
Sm-152 Colony
Mound
Site: Weed-free A
Day: 2
Date: 29 July 1986
Max. Dist. Sm-152: 10.3 m
% Sm-152 S. invicta: 11.3
% S. invicta: 67.7
% P. vividula: 11.3
% P. hoffeens: 9.7

Figure 1,E-F.

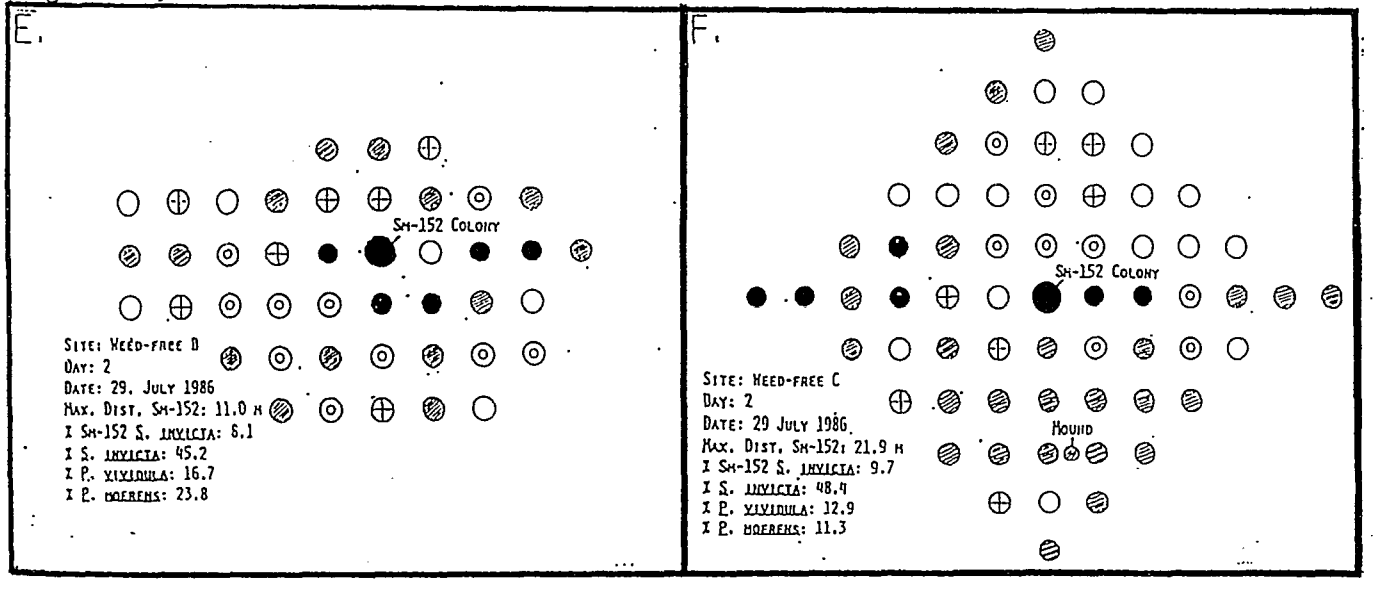

Fig. 1. Solenopsis invicta foraging territories in weedy (A-C) and weed-free (D-F) sugarcane habitats on July 29, 1986. The rows of sampling stations were placed on alternate rows in a 3.65 X 3.65 m grid pattern. The weed regime and site, maximum distance Sm-labeled ants were found from the mound, and the relative amount of sampling stations occupied by the Sm-labeled S. invicta, total S. invicta, P. vividula, and P. moerens are indicated.

Center, College Station, TX, for neutron irradiation (Knaus and Van Gent 1987, Knaus 1988) at one megawatt in a calibrated flux of ca. 1 X 10^{13} thermal neutrons/cm^2/sec for two min per 2-dram vial in a TRIGA research nuclear reactor. Each 2-dram vial was delivered to the reactor core through a CO_2-driven pneumatic transfer system. A lithium-drifted germanium crystal semiconductor detector linked to a multichannel analyzer on a setting for 0.103 MeV gamma ray counting was used to measure the radioactive decay ($T_{\frac{1}{2}}$=46.7 h) of Sm-153 (from the irradiation of Sm-152, which comprises 26.7% of the seven collective isotopes of samarium) to the stable Eu-153 in each small polyvial. Ant samples were determined to be labeled with Sm when counts per min were 2X background radiation.

SAS procedures (SAS Institute 1979) were used to delineate relationships among weed growth, S. invicta foraging areas and populations, and the foraging activities of other ant species. Differences between the weed regimes for soil surface- and sugarcane stalk-associated arthropod numbers, fire ant mound density, weed biomass (from six replicates), and information collected from the sampling grids (three replicates) were analyzed as completely randomized designs using the unpaired t-statistic.

RESULTS

Total weed biomass ($\bar{x}$±SE) in the W habitats was 61±12 g/0.5 m^2, represented by 7% Brachyaria platyphylla Nash, 6% Cynodon dactylon Pers., 85% Digitaria sanguinalis Scop., and 2% Panicum dichotomiflorum Michx. Collective soil surface-associated prey arthropods were reduced 46% (t=4.4; df=46; MSE=50.1; P≤0.0001) in WF habitats when compared with

W areas. The relative abundances of soil surface-associated arthropod groups in the W and WF systems were Gryllidae, 74 and 72%; Coleoptera (Chrysomelidae, Heteroceridae, and Scarabaeidae), 12 and 22%; nonpredaceous Hemiptera (Cydnidae, Lygaeidae, and Pentatomidae), 1 and 0.4%; Cicadellidae, 11 and 4%; and lepidopterous larvae, 1 and 1%, respectively. The weed foliage had 127±11 prey arthropods per 20 sweeps; 4% Orthoptera (Acrididae, Tettigoniidae), 4% Coleoptera (Chrysomelidae, Curculionidae), 12% Lygaeidae, 12% Pentatomidae, 54% Cicadellidae, 8% Diptera, and 6% lepidopterous larvae.

S. invicta mounds were 80% ($t=7.0$; $df=22$; $P\leq0.0001$) more dense in W ($\bar{x}=197\pm20$/ha) than in WF ($\bar{x}=40\pm9$/ha) habitats. Pitfall trap-collected S. invicta numbers in the W versus WF habitats were 9±5 and 4±0.6, respectively. S. invicta workers were found on 7.5±1.8 and 4.6±1.9% of the total sugarcane stalks examined in the W and WF habitats, respectively. Significantly more ($t=3.2$; $df=16$; $P\leq0.006$) of the baited sampling stations, however, contained S. invicta foragers in the W (64±3%) than the WF (49±4%) areas.

Samarium-labeled S. invicta were found to forage in 6.4±0.7% of the sampling stations which was significantly less ($t=2.6$; $df=16$; $P\leq0.02$) than the 9.0±0.7% that attracted S. invicta workers in the WF regimes (Fig. 1,A-F). S. invicta workers traveled a maximum distance from the mound of 8.9±1.3 m while the WF colonies foraged significantly ($t=2.4$; $df=16$; $P\leq0.03$) farther to 13.1±1.2 m. The relative foraging areas of the Sm-labeled fire ant colonies and total S. invicta were not significantly correlated.

Two other formicid species, Paratrechina vividula Nylander and Pheidole moerens Wheeler, were encountered in bait stations (Fig.

1,A-F) not utilized by S. invicta (n=266) (except on two occasions when P. vividula and S. invicta were observed together, not shown in Fig. 1). P. vividula was found in 7.7±1.2% of the W sampling stations but was more common ($t=3.0$; $df=16$; $P \leq 0.008$) in WF areas ($\bar{x}=14.0\pm1.7\%$). A significant correlation ($r=-68.5$; $P \leq 0.02$) was observed between the relative number of sampling stations occupied by S. invicta and by P. vividula, respectively. Differences between the relative numbers of sampling stations occupied by P. moerens in W (14.9±1.3%) and WF (14.9±1.9%) habitats were not detected.

DISCUSSION

Ali et al. (1984) counted 36% more S. invicta workers foraging from nests in weedy sugarcane habitats than in areas with significantly fewer prey items (WF). Our study demonstrated that pitfall-collected and sugarcane stalk-associated S. invicta numbers tended to be higher and foraging activity was 25% more area-intensive in W than WF systems.

INAA (for review, see Showler et al. 1987b) with the Sm marker was an effective method for the delineation of S. invicta foraging areas without the introduction of radioactivity into the environment, and particularly in food producing crop systems. The rare earth tag was probably passed throughout each labeled colony by trophallaxis (food exchange) (Howard and Tschinkel 1981). S. invicta colonies have been shown to have discrete foraging territories that changed daily (Showler et al. 1987a) and seasonally (Wilson et al. 1971). Our experiment demonstrated that S. invicta territories extended across sugarcane furrows and that W prey abundance resulted in the significant 29 and 32% reductions in territorial size and maximum distance foragers traveled

from their mounds, respectively. The failure to detect a correlation between Sm-labeled and total S. invicta foraging activities indicated that territorial size was reduced due to higher prey density, which permitted greater fire ant colonization. Increased S. invicta colonization has been associated with lower populations of other Formicid species (see review by Showler and Reagan 1987b); this experiment demonstrated that the high S. invicta populations in W habitats occurred at the expense of the abundance of P. vividula, but not that of P. moerens.

We conclude that weed diversification sustained higher densities of S. invicta colonies in response to increased of food availability. The intensified area-wide fire ant foraging activity in W habitats permitted the reduction of territorial size required to support each colony. The weed-related intensification of S. invicta foraging was at least partially responsible for the significant reductions in sugarcane borer injury to the crop and higher sugar yields observed by Showler et al. (1987a). Although INAA is time-consuming and expensive, it is and effective and sensitive method for conducting studies in a food producing agroecosystem.

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SUMMARY

Long-term studies using large field plot designs, surveys, and numerous sampling methods (pitfall traps, bait stations, sweep net collections, sugarcane stalk inspections, weed quadrats, and soil cores) were used to observe a plexus of interrelationships in the sugarcane agroecosystem. An overview of the collected data indicates that the sugarcane agroecosystem should be described from a broad holistic perspective as a complete, interacting unit. Ecological relationships among weeds, nematodes, arthropods, sugarcane mosaic virus (SCMV), and the sugarcane (variety: CP 74-383) crop, itself, included competition, trophic web relationships, and biochemically mediated associations among host plants and phytophagous organisms. The use of herbicides, a broad-spectrum nematicide-insecticide, and a reportedly selective pyrethroid insecticide for the control of the sugarcane borer, Diatraea saccharalis (F.), allowed the ecological and economic assessment of eight possible pest management strategies: 1) weedy, no aldicarb, no insecticide, 2) weedy, aldicarb-treated, no insecticide, 3) weed-free, no aldicarb, no insecticide, 4) weed-free, aldicarb-treated, no insecticide, 5) weedy, no aldicarb, insecticide-treated, 6) weedy, aldicarb- and insecticide-treated, 7) weed-free, no aldicarb, insecticide-treated, and 8) weed-free, aldicarb- and insecticide-treated. The use of radiotracer and instrumental neutron activation analysis (INAA) methods enabled the study of Solenopsis invicta Buren, the key predator of D. saccharalis, foraging area responses to floral complexity, flooding, nest relocation, and intraspecific competition.

Weed biomass in the Assumption Parish sugarcane field was composed of the following species: Brachyaria platyphylla Nash, Echinochloa spp.,

Cynodon dactylon Pers., Panicum dichotomiflorum Michx., Cyperus esculentis L., and at least 85% was Digitaria sanguinalis Scop. Total summer annual weed biomass in the weedy habitats was shown to increase until mid-season, then to decline with the closure of the sugarcane canopy. Floral complexity was associated with higher densities of prey and predatory arthropod fauna on the soil surface, weed foliage, and sugarcane stalks and foliage. Sugarcane borer predators were primarily composed of S. invicta, other formicids, and Araneae, and to a lesser extent, Carabidae, Staphylinidae, and Dermaptera. Weedy plots were shown to sustain more S. invicta mounds per ha (86%, 78%; 1985, 1986). Using INAA and the nonradioactive rare earth element, samarium, as a tracer, imported fire ant colonies were labeled in weedy and weed-free sugarcane habitats. Colonies in the weedy areas foraged in 6.4% of the sampling stations and traveled an average maximum distance of 8.9 m from the mound. The weed-free Sm-labeled colonies occupied 9.0% of the sampling stations and traveled an average maximum distance of 13.1 m from the mound. The significant 28% reduction in the foraging territory size associated with weedy habitats was a result of more dense S. invicta prey populations which permitted greater S. invicta colonization and 25% more foraging activity per unit area (as determined by bait station transects). S. invicta foraging activity, however, was negatively correlated (r=-0.69) with the occurrence of Paratrechina vividula Nylander (another formicid species encountered in Louisiana sugarcane), probably due to interspecific competition.

The weed-associated increase of predator populations was responsible for the reductions in D. saccharalis injury to the crop (28%, 42%; 1985, 1986). Although weed competition caused declines in

sugarcane stand density (24%, 18%; 1985, 1986) and biomass (19%, 15%; 1985, 1986), and resulted in reduced (15%, 14%; 1985, 1986) sugar yields, weedy sugarcane without chemical sugarcane borer control produced 15 and 76% more net income per ha than similar weed-free areas. Return investment ratios (-1.95, -1.98; 1985, 1986) indicated that, for every dollar spent on weed control in the absence of chemical sugarcane borer management tactics, two dollars were lost in terms of profit.

By taking soil core samples from directly below the sugarcane stools, and in the gaps between stools, the sugarcane field was found to harbor the following nematode groups: ring, Criconemella curvata and C. onoensis; root-knot, Meloidogyne incognita and M. javanica; stubby root, Paratrichodorus minor; lesion, Pratylenchus zeae; reniform, Rotylenchus reniformis; and stunt, Tylenchorhynchus annulatus. Lance, Hoplolaimus columbus; and spiral, Helicotylenchus dihystera and H. pseudorobustus composed less than 1% of the total phytophagous nematode populations. Although the nematode densities were variable over time, weedy interstool gaps failed to sustain more phytophagous nematodes than were found in unvegetated gaps, except for Criconemella spp. Even augmented phytophagous nematode infestations failed to influence weed biomass or the relative biomass of each weed species. Nematode population trends on sugarcane required nearly one full growing season to become apparent, and the trends usually carried over into the ratoon season. By 1986, Criconemella spp., P. minor, T. annulatus, and total phytophagous nematode abundances were 49, 79, 26, and 40% greater ($P \leq 0.01$), respectively, on weedy sugarcane than in weedy gaps. Similarly, weed-free sugarcane harbored more Criconemella spp., P. minor, T.

annulatus, and total phytophagous nematodes in both the plant and the ratoon crops.

Sugarcane in the weedy habitats was infested by less Criconemella spp., Meloidogyne spp., T. annulatus, and total phytophagous nematodes than weed-free sugarcane after the middle of the first growing season. P. minor, P. zeae, R. reniformis, and total nonphytophagous nematode populations on sugarcane were not affected by the growth of weeds. Of the 17 free amino acids (FAAs) detected in preharvest sugarcane, 15 were significantly lower in weedy areas. Host plant FAA accumulations have been demonstrated, by other researchers (chapters II and III), to be related to host plant stress and changes in FAA levels may play a role in the biochemical mediation of plant susceptibility to phytophagous organisms, including nematodes. Sugarcane mosaic virus- (SCMV) stressed sugarcane was found to accumulate less of 13 and 5 FAAs in weedy and weed-free habitats, respectively. A significant weed-virus interaction ($P \leq 0.001$) was detected for free cysteine; T. annulatus populations were highly correlated ($r=0.59$, $P \leq 0.001$) with the weed- and virus-induced changes in free cysteine. Sugarcane with supplemented phytophagous nematode populations, including Meloidogyne spp., accumulated significantly less free cysteine, histidine, proline, and serine. Thus, it apprears that the stresses induced by nematodes, weeds, and SCMV each contribute to alterations in sugarcane FAA levels. Criconemella spp., Helicotylenchus spp., T. annulatus, and total phytophagous nematodes were found to be positively correlated with one or more FAAs, while P. zeae infestations were negatively correlated ($r=-0.53$) with free tyrosine accumulations. It was concluded that infestations of some sugarcane nematodes were related to FAA concentrations. The FAA

accumulations were also related to biotic stresses including weed, SCMV, and even nematode pressure. Weed stress was found to be associated with the greatest reductions in FAA concentrations, followed by the SCMV- and nematode-related pressures. Unlike weed competition, the augmented nematode infestations did not result in sugarcane yield reductions.

To investigate the impact of chemical nematode control on sugarcane nematode populations, arthropod fauna, weed growth, and sugarcane production, granular aldicarb was soil incorporated along the sugarcane rows in the early spring of each year. The carbamate nematicide-insecticide was shown to be a broad-spectrum pesticide, but failed to influence weed biomass and the relative abundance of each species. Soil surface-, weed-, and sugarcane foliage-associated plant-sucking insects, in particular, were diminished for up to 10 weeks after aldicarb was applied. Regardless of the weed regime used, soil surface-, weed-, and sugarcane stalk-associated predator densities were decreased by the nematicide. S. invicta colonization was reduced (77%, 58%; 1985, 1986) and fewer workers were collected on the weeds (48%, 1986) and on the sugarcane stalks (59%, 66%; 1985, 1986) where early instar D. saccharalis larvae commonly develop before entering the sugarcane. The reduction of predatory arthropods in aldicarb-treated areas was associated with increased D. saccharalis injury to the crop (19%, 33%; 1985, 1986).

Aldicarb was shown to provide inconsistent control of phytophagous nematodes, including Criconemella spp., Helicotylenchus spp., P. minor, and P. zeae. Free proline, frequently related to nematode populations by other researchers, was significantly more concentrated (18%) in the aldicarb-treated sugarcane, possibly in response to the alleviation of

nematode-induced pressure. The aldicarb-associated change in free proline may impinge upon host plant resistance to other phytophagous organisms.

The nematicide-insecticide was not associated with reductions in sugarcane stand density, biomass, and sugar production. Sucrose concentrations were significantly lower, but by only 4 and 5% in 1985 and 1986, respectively. In plots where D. saccharalis control was not provided, net income per ha was lower in nematicide- and/or herbicide-treated areas. Return investment ratios, where aldicarb was applied in the absence of effective sugarcane borer control, indicated that expenditures on aldicarb for nematicide control were not profitable.

The impacts of D. saccharalis control using a reportedly selective pyrethroid insecticide, fenvalerate, applied the currently recommended economic threshhold levels, were determined by sampling for prey and predator arthropod fauna, and by assessing the injury to the crop and yield measurements. The insecticide reduced weed-associated prey arthropods and soil surface- and cane stalk-associated predators, including S. invicta. Fenvalerate reduced sugarcane foliage-associated Cicadellidae populations (77%, 55%: 1985, 1986), but yellow sugarcane aphid, Sipha flava (Forbes), infestations were greater (197%, 64%; 1985, 1986) than in fenvalerate-free habitats. The specific causes for the proliferation of S. flava on the insecticide-treated sugarcane have not been determined.

Although fenvalerate did reduce some predatory arthropods, the insecticide was effective at reducing D. saccharalis infestations in the leaf sheaths (92%, 68%; 1985, 1986) and injury to the crop (93%, 70%; 1985, 1986) regardless of the weed habitat or the nematode control

regime used. By the first ratoon season, sucrose concentrations and commercial sugar yields were significantly greater in the fenvalerate-treated areas by 4% and 9%, respectively. Effective protection of the crop against the sugarcane borer resulted in overall increases in net dollar returns (18%, 57%; 1985, 1986) and return investment ratios indicated that the judiciously timed application of an effective insecticide was economically profitable. The simultaneous release of the crop from both weed- and sugarcane borer-induced pressures was the most economically sound pest management strategy. Effective integrated management of D. saccharalis in Louisiana sugarcane should discourage the use of broad-spectrum, long-residual pesticides, but incourage the maintenance of subcompetitive weed growth to enhance natural enemy populations, and the judicious application of effecient and selective insecticides.

During the examination of S. invicta territories, the ecological interactions of the imported fire ant in the southeastern United States were studied. Due to facets of its biology, such as mass foraging, a venomous sting, territorial behavior, large colony size, and alate dispersal, S. invicta has become the predominant formicid throughout most of its North American range. Already well-ensconced and interacting with its environment on many levels, the imported fire ant appears unrestricted by the biotic communities in which it lives despite man's concerted efforts at imposing control. Field studies additionally have demonstrated the fire ant's power of resurgence following insecticidal control applications. While some view the imported fire ant as a "pest," this epithet has been cast into doubt as researchers continue to yield information pertaining to S. invicta's broad

interactions and beneficial implications within various agroecosystems. The potential of the imported fire ant as a beneficial component of our ecosystem may, upon further investigation, reveal additional advantages to its accidental introduction.

Further, the possible applications of radiotracer methods in the study of insect ethology and ecology were investigated. Isotope markers can be radioactive or nonradioactive and can include a wide diversity of nuclides that may be conservative (mimic biologically essential elements) or nonconservative. Detectable radiations include alpha particles, beta particles, and gamma or X-rays, or combinations thereof. Radiotracer half-lives range from hours to years, and stable-activable tracers can be permanent. Methods of application to the system of interest include injection, dipping, wire or disc attachments, paints, ingestion, trans-life-stage transmission, and water culture. Labels have been ingested from labeled baits, other insects, living plants with topically applied or translocated labels, blood, and living host animals. Radiolabels have been transferred to the insect life stage of interest by being retained through molts and metamorphic processes.

The unit labeled may range from selected individuals to entire populations and ecosystems. Communities studied have been aquatic, terrestrial, soil- or wood-limited, or combinations thereof. It is possible to design experiments for studying each and combinations of the following behaviors and ecological interactions: dispersal and movement patterns, territoriality, food handling and consumption, vector-parasite associations, and trophic webs.

In addition to using INAA in the sugarcane agroecosystem as a sensitive alternative to radiotracer methods for studying the

interaction of S. invicta foraging areas with weed and prey densities, radiotracers Mn-54 and Zn-65 were employed to monitor the foraging area dynamics of two adjacent imported fire ant colonies daily for 20 consecutive days. Nest relocation and the close proximity of other S. invicta colonies were observed to be associated with territorial patterns that may provide a unique perspective for the study of S. invicta ethology and interactions with the environment, and for unraveling other relationships inherent to the sugarcane agroecosystem.

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APPENDICES

APPENDIX A

ECOLOGICAL INTERACTIONS OF THE RED IMPORTED FIRE ANT IN THE SOUTHEASTERN UNITED STATES

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INTRODUCTION AND BIOLOGY

A stinging social insect indigenous to the Mato Grosso region of Brazil, parts of Paraguay and Argentina, the red imported fire ant, Solenopsis invicta Buren, arrived in Mobile, Alabama in the 1929 (Lofgren 1986) and has since proliferated to colonize nine southeastern states (Buren et al. 1974, Lofgren et al. 1975, Cantor 1981, Mirenda and Vinson 1981, Francke et al. 1985) and Puerto Rico (Buren 1982). The queens initiate colonies following nuptial flights that occur each month of the year with peak flight activity between May and August (Markin and Dillier 1971, Markin et al. 1972, 1973, Morrill 1974, Lofgren et al. 1975, McCarty et al. 1980, Tschinkel 1986) and colonies can produce 3-5 thousand queens per year (Lofgren and Weidhaas 1972). Fire ant reproduction is usually relegated to a single queen per colony, although polygynous colonies have been reported in Texas, Georgia, and Mississippi (Hung et al. 1974, Glancey et al. 1975, Adams et al. 1976, Wilson 1978, Mirenda and Vinson 1982, Fletcher 1983), and colony reproduction can occur within one year of colony establishment (Tschinkel 1986). While the queens are morphologically distinct, workers range in length from 2-6 mm and have not been successfully categorized into definite subcastes (Wilson 1978, Mirenda and Vinson 1981).

Fire ants establish colonial mounds with subterranean galleries that can sustain populations of 50,000-230,000 workers (Markin et al. 1973, Horton et al. 1975, Lofgren et al. 1975, Tschinkel 1986). Mound densities of up to 2,500, but usually not over 250, mounds per ha have been observed, usually in pastures, cultivated regions, unattended woodlands, and disturbed habitats (Green 1952, Lofgren et al. 1975,

Mirenda and Vinson 1981, Wojcik 1983, Tschinkel 1986). Tunnels radiate from each mound and are located 2-12 mm below ground level; one colony's tunnel system was found to collectively extend 84 m (Markin et al. 1975). Intermittently situated tunnel exits facilitate surface foraging (Horton et al. 1975, Lofgren et al. 1975, Markin et al. 1975) even in water-saturated soil conditions (Showler et al. 1988) common to the fire ant's North American habitat. From these tunnels, fire ants feed on a wide diversity of insects, spiders, mites, molluscs, plant material (Eden and Arant 1949, Wilson and Oliver 1969, Ali et al. 1984), honeydew produced by homopterous insects (Hays and Hays 1959, Nelson et al. 1971, Nickerson et al. 1974, Wilkinson and Cellman 1979, Reilly and Sterling 1983), and nectar (Agnew et al. 1982). Mass foraging at specific sites is instigated by a trail pheromone secreted by an accessory gland and extruded through the stinger of scout workers (Wilson 1959, Wilson 1962, Wilson 1971, Vander Meer 1986,) along the tunnel systems (Horton et al. 1975). Recruitment time relative to food sources has been shown to decrease with increasing distance from the mound (Horton et al. 1975) such that food gathering efficiency is maximized within a colony's foraging range. Using ant-ingested dyes to distinguish between 6 adjacent colonies, Wilson et al. (1971) determined that the fire ant exhibits territorial behavior, as little movement or communication between colonies was observed. Showler et al. (1988) employed radiozinc-65 and radiomanganese-54 to monitor the foraging behavior of two adjacent colonies for 20 consecutive days, and fire ant territoriality was shown to be both discrete and temporally dynamic. Fire ant foraging territories border one another so it is conceivable that a heavily infested tract of land could exist as a contiguous

patchwork of discrete territories. Transect studies have shown that 92-100% of baited sampling sites can be monopolized by S. invicta (Baroni-Urbani and Kannowski 1974).

The fire ant possesses traits that have contributed to its rapid adaptation to the southeastern United States. These major characteristics are:

i) A general omnivorous food habit which increases the probability of locating suitable dietary resources.

ii) Mass foraging recruitment that permits rapid and efficient removal of discovered food items.

iii) Massive aerial dissemination of reproductive females which facilitates maximimum dispersal of the species. iv) Competitive territorial behavior which serves to protect the nest and to secure foraging areas for continued use.

v) The ability to utilize foraging areas in water-saturated soil which permits access to established foraging territories and allows colony survival in such adverse conditions.

vi) Tunneling behavior that offers protection from trail disruption to foraging sites.

vii) Territorial shifting over time which permits efficient use of foraging areas when specific sites have been depleted.

viii) A stinging mechanism that has utility for both capturing prey and defending against intruders.

ix) A large colony population size which increases foraging potential and can sustain many casualties during intraspecific confrontations.

The South American habitat to which the fire ant is indigenous supports a complex of pathogens (Allen and Silvera-Guido 1974, Jouvenaz

et al. 1977, Knell et al. 1977, Jouvenaz and Anthony 1979, Jouvenaz et al. 1980, Jouvenaz and Lofgren 1981) that infect 20-25% of the colonies (Jouvenaz et al. 1977) and may be a regulatory factor on fire ant populations (Allen and Silvera-Guido 1974, Jouvenaz et al. 1977, Wojcik 1986). In contrast, surveys have shown that disease among fire ants in the southeastern United States is rare; only 9.2% of the colonies examined were found to host a benign or mildly pathogenic fungus (Jouvenaz and Anthony 1979) most commonly encountered in areas long infested with S. invicta (Jouvenaz et al. 1977). Unchecked by disease in the United States, fire ant colonies exist at higher densities than in South America (Williams and Whitcomb 1973, Wojcik 1986). Considering the fire ant's competitive advantages and current absence of virulent population-limiting pathogens, S. invicta would be expected to interact in many ways with its new domain. Current understanding of the fire ant's relationships with its environment will be subsequently addressed in this review.

INTERACTIONS

Other Ants

Since its introduction, the fire ant has been implicated as a significant competitive force upon the distribution of other formicid species, and species that had previously predominated were frequently displaced (Travis 1938, Baroni-Urbani and Kannowski 1974, Howard and Oliver 1978, Mirenda and Vinson 1981, Phillips et al. 1986). Laboratory experiments for the observation of interspecific confrontational behavior have yielded mixed results. S. invicta inflicted twice the mortality on a species of red wood ant Formica integra Nylander than the

fire ant itself sustained (Wilkinson et al. 1975). Conversely, Bhatkar et al. (1972) showed that Lasius neoniger Emery (a poneroid ant), which used mandibular defense and a secretion sprayed from the acidopore of the gaster into the fire ant's facial region, vigorously attacked and killed S. invicta workers. Each L. neoniger combatant could receive 3-4 fire ant stings before the advent of lethal effects. About 2.4 fire ants were eliminated for each L. neoniger killed, and field observations indicate that the fire ant is not as dominant a colonist where L. neoniger exists. This situation, however, is known to be manifest only in a limited area of Florida, and the same study (Bhatkar et al. 1972) showed that L. neoniger colonies eventually succumb to attrition because of the sheer populational magnitude of fire ant colonies. Similarly, Phillips et al. (1986) demonstrated that when colony populations are equal, S. invicta did not impinge upon the foraging abilities of Pheidole dentata Mayr. It appears that S. invicta is most vulnerable to attack when it's solitary queens alight after a nuptial flight and before a colony is generated (Reilly and Sterling 1983). Dolichoderine pyramid ant, Conomyrma insana Buckley, workers frequently prey upon such S. invicta queens but, like L. neoniger, C. insana has a distribution limited to parts of Florida (Nickerson et al. 1975, Howard and Oliver 1979). After mirex treatments where the fire ant was poorly established, C. insana and S. invicta resurgences occurred such that both species dominated at the expense of the other soil inhabiting ants (Summerlin et al. 1977).

Field studies in the southeastern United States portray the fire ant as the dominant Formicid species. This is illustrated by fire ant resurgences 7-12 months after toxic bait applications (Howard and Oliver

1978, Brown 1980, Mirenda and Vinson 1981, Apperson et al. 1984) that, in one study, exceeded pretreatment populations (Summerlin et al. 1977). All attempts to control S. invicta with mirex simultaneously suppressed other ant species such as Conomyrma flavopecta M. R. Smith (Adams et al. 1981), Diplorhoptrum sp. (Buren 1983), Iridomyrmex pruinosum Roger (Nickerson et al. 1975), Monomorium minimum Buckley (Markin et al. 1974), Nylanderia spp. (Howard and Oliver 1978), Odontomachus haemotodis Roger (Adams et al. 1981), Paratrechina bourbonica Forel (Adams et al. 1981), P. dentata (Adams et al. 1981, Summerlin et al. 1977), P. floridana Emery (Adams et al. 1981), Pogonomyrmex badius Latreille (Markin et al. 1974), Solenopsis geminata F. (Adams et al. 1981, Summerlin et al. 1977), S. xyloni McCook (Markin et al. 1974), Strumigenys membranifera Emery (Adams et al. 1981), and Trachymyrmex septentrionalis McCook (Summerlin et al. 1977). Buren (1983) also described the fire ant's resurgence powers following environmental disruptions, including insecticide applications. It is, then, not surprising that Whitcomb et al. (Whitcomb et al. 1972) and Reagan et al. (1972) found a less diverse ant fauna in S. invicta infested soybean and sugarcane fields, respectively. Stimac (1983) further suggested that the use of chemical treatments for fire ant eradication has contributed to the proliferation of S. invicta due to fire ant resurgences at the expense of other ant species. White (1980) showed, too, that as levels of predation increased in sugarcane ratoon crops, significantly stronger negative correlations became apparent between the fire ant and other ants. Similar investigations in uncultivated land have demonstrated that the fire ant is competitively superior to most native and other introduced formicid species (Baroni-Urbani and Kannowsky 1974, Hung

1974, Glancey et al. 1976, Hung et al. 1977, Moody et al. 1981, Apperson and Powell 1984).

After dominating it's niche, the fire ant appears to reach an equilibrium with native ant species (Wilson 1971, Glancey et al. 1976). Cohabitation of an area with the aggressive and competitive fire ant is a result of strategies by other species that avoid direct physical confrontation (Markin et al. 1974). The indigenous species can persist as a result of i) exploitation of other resources in habitat-diverse environments (Buren 1983, Odum 1971), ii) chemical repellency such as that exhibited by M. minimum (Baroni-Urbani and Kannowski 1974, Markin et al. 1974), iii) high mobility (Aphaenogaster rudis Emery can move faster than S. invicta) (Buren 1983), or iv) proximity to resources (small ants would require smaller foraging ranges). The latter two strategies each contribute to the reduction of recruitment time to resources. Phillips et al. (1986) demonstrated that recruitment time is nearly identical for three Formicid species sympatric with the fire ant: Forelius foetidus Buckley, M. minimum, and P. dentata (these were the only taxa they compared).

Other Insects and Vertebrates

Few insects are exempt from fire ant predation, including ant lions (Neuroptera: Myrmeliontidae) (Lucas and Brockman 1981) which normally consume formicids. Six species of birds have even been verified as occasional fire ant prey (Travis 1938, Kroll et al. 1973, Parker 1977, Delnicki and Bolen 1977, Ridlehuber 1982, Adams 1986) and it has been speculated that S. invicta is a key factor in depleting nine reptile species along the Alabama coast (Mount et al. 1981).

On the other hand, solitary post-nuptial flight fire ant queens are prone to attack by several species of insects and birds. Whitcomb et al. (1973) observed four dragonflies Avax junius Drury, Pachydiplax longipennis Burmeister, Somatochlora provocans Calvert, Tramea carolina L.; three birds, the chimney swift Cahaeura pelagica L., the eastern kingbird Tyrannus tyrranus L., the eastern bobwhite Colinus virginianus virginianus L.; one lycosid spider Lycosa timuga Wallace; one earwig Labidura riparia Bollas; and a tiger beetle Cicindela punctulata Oliver, actually feeding on unprotected queens.

Aside from the above mentioned predator and prey relationships, there exist nonlethal associations between S. invicta and other insects. While aphids have been identified as a common dietary component (Wilson and Oliver 1969, Ali et al. 1984), homopterous insects are frequently tended for honeydew by fire ants (Hays and Hays 1959, Neilson et al. 1971, Nickerson et al. 1974, Sterling et al. 1979, Wilkinson and Sterling 1979, Scarborough 1984). Reilly and Sterling (1983) found fire ants and Aphis spp. in east Texas cotton fields to be highly aggregated together.

Although fire ants in South America host 14 Pseudodacteon spp. (Diptera: Phoridae), two Solenopsis spp. (Hymenoptera: Formicidae), and Orasema spp. (Hymenoptera: Eucharitidae) (Hays 1958, Williams and Whitcomb 1973), such parasitic associations have not been reported in the United States. Several insects, however, have been excavated from fire ant nests, and most of them are indigenous to South America. Myrmecosaurus ferrugineus Bruch (Coleoptera: Staphylinidae), native to Argentina (Collins and Markin 1971, Frank 1977), has been located in Georgia, Mississippi (Collins and Markin 1971), Alabama, Florida, and

Louisiana (Frank 1977). Wojcik (1980) did not observe M. ferrugineus predation on S. invicta eggs, larvae, pupae, workers, or queens, and noted that this rove beetle repeatedly attempted to elicit trophallactic (food exchange) behavior from workers within the nest. An Argentinian tenebrionid beetle Poecilocrypticus formicophilus Gebien that feeds on plant and fungal matter has been discovered within fire ant nests in Alabama, Florida, and Mississippi, but little is known regarding it's biology except that it appears to be an occasional scavenger of ant galleries (Steiner 1982). A scarab beetle Myrmecaphodius excavaticollis Blanchard from Argentina (Woodruff 1973) was found in association with 98% of the fire ant nests examined in Alabama, Florida, Georgia, Mississippi, North Carolina, and Texas, but little is known regarding it's relationship with the fire ant (Collins and Markin 1971). Collins and Markin (1971) listed an undescribed Thysanura sp. that inhabits S. invicta nests in Florida, Mississippi, and Texas, but little is understood about its biology. A planthopper Oliarus vicarius Walker (Homoptera: Cixiidae), usually a denizen of subterranean rotted wood, was discovered in abandoned Georgia fire ant mounds. It has been speculated that the introduction of S. invicta to the United States may have a beneficial impact on this planthopper's proliferation by increasing its habitat range (Sheppard et al. 1979).

One undescribed species of Uropodid mite attaches to the upper surface of the thorax and occasionally on the legs, antennae, and abdomen of alate female fire ants. This mite was observed on fire ant workers only in weakened colonies that harbor depleted alate female populations (Collins and Markin 1971). Two other mites Oplitis moseri Hirschmann and O. virgilinus n. sp. have been described in association

with S. invicta nests is South Carolina and North Carolina, respectively (Hunter and Farrier 1976).

While providing sustenance to certain North American insects and birds, the fire ant has multiplied throughout the southeastern United States. Native Homoptera have adapted to the honeydew collecting habits of S. invicta, and several South American beetles and a few indigenous insects and mites have been accoutred with new, and probably permanent, niches in North America.

Agriculture

The fire ant has become firmly enscónced within the biotic communities it shares. In doing so, this insect has exerted a measurable impact upon man, particularly in agroecosystems. Experiments conducted in various crop systems have illustrated the fire ant's capacity to be viewed as both a detrimental and a beneficial component in agriculture.

Lofgren et al. (1975) has categorized S. invicta as a "nuisance pest" due to its habit of erecting mounds and its stinging behavior. Adams (1986) reported that 100-125 mounds per ha are frequently associated with corn and soybean fields. These mounds were implicated in damage to harvesting equipment and to the reducion of harvestable soybean yields (Adams et al. 1976, Adams et al. 1977, Apperson and Powell 1983) by as much as 5.1 hl per ha when there were 49-176 mounds per ha (Lofgren and Adams 1981). Kidd and Apperson (1984), however, reported that mound interference with mechanical harvesters "accounts for only a small portion of these losses." Using P-32 inoculated soybean seedlings, Smittle et al. (1983) found that fire ants obtained

the radiolabel, indicating that S. invicta may contribute to stand reduction by feeding on the young plants. Phosphorus-32, however, has been shown to move across arthropod trophic levels (McCarty et al. 1980) and thus may have been transferred first to obligate herbivores that were subsequently devoured by fire ants. Lyle and Fortune (1948) reported that the fire ant was a major agricultural pest in Mississippi. Farmers polled in 1949 implicated the fire ant as a deleterious agent in corn, peanuts, beans, potatoes, and cabbage (Wilson and Eads 1949), and another early report noted that S. invicta consumed corn seedlings (Yates and Smith 1935). More recently, Adams (1983) reported a 50% reduction of seedling eggplant as a result of fire ant infestation. Adams (1986) also found that up to 35% potato losses in Florida were attributed to S. invicta and approximately 2.7% of a Florida citrus orchard was girdled and killed by fire ants. S. invicta has been reported to reduce citrus flowering by 50% as a result of fire ant feeding near the calyx of the blossoms (Adams 1986). Fire ant feeding was additionally responsible for damaging 40.8% of the developing citrus fruit; after fruit-set S. invicta consumed new shoot growth and pruned the trees. Experiments employing P-32 labeled citrus trees indicated that S. invicta fed directly on the flowers, sap, and various other tissues (Adams 1986). Germinating longleaf pine seedlings suffered a 32.8% stand reduction as a result of fire ant foraging (Campbell 1974). In contrast, Hays and Hays (1959) revealed that S. invicta is primarily entomophagous, and that colonies practiced cannibalism rather than devour plant material which included cucumber, squash, watermelon, English pea, bean, soybean, corn, Irish potato, cabbage, tomato, cantaloupe, pine, pansy, marigold, and cotton. Among the plants they

studied, only okra was shown to sustain damage (15%) inflicted by S. invicta; the calyx of okra flowers has been identified as both an attractant to and a dietary item of foraging workers (Wilkinson and Cellman 1979).

Unlike the preceding reports, other studies depict the fire ant as a beneficial component of agroecosystems (Reagan 1986). Soil analysis of pasture mounds demonstrated that mounds, in many instances, were enriched with phosphorus, potassium, calcium, and magnesium (Herzog et al. 1976). This alteration in soil chemistry significantly increased proteins, carotene, and phosphorus in grasses rooted on the mounds. Onthophagus gazella F. (Coleoptera: Scarabaeidae) reduced egg and larval habitats for the horn fly, Haematobia irritans L. (Diptera: Muscidae), by decomposition and incorporation of dung into pasture soil (Summerlin et al. 1977). The fire ant was shown to suppress horn fly populations (Howard and Oliver 1978) even more than O. gazella alone (Summerlin et al. 1977). Harris and Burns (1972), using mirex to exclude S. invicta from pastures, showed that the presence of S. invicta significantly decreased the tularemia-vectoring lone star tick, Amblyomma americanum L., a potentially serious pest to humans, livestock, and wildlife. Vinson (1972) reported that the fire ant collected seeds of dallisgrass, Paspalum dilatatum Poir., but only those that hosted ergot.

Fire ant infestations have been characterized as beneficial in field crops as well as in pastures. Although the fire ant has been shown to reduce carabid beetles (Brown and Goyer 1982) and other predators (Whitcomb et al. 1972) in soybeans, Whitcomb et al. (1973) reported fire ant predation on the soybean looper, Pseudoplusia includens Walker, the velvetbean caterpillar, Anticarsia gemmatalis

Hubner, and the southern green stink bug, Nezara viridula L., and Snodgrass (1976) noted that fire ants also feed on the green cloverworm, Plathypena scabra F. Sterling et al. (1979) presented data indicating that S. invicta did not suppress entomophagous insect and spider populations in the cotton agroecosystem. The fire ant has instead been identified as an important predator in cotton by feeding on bollworm Heliothis virscens F. eggs (McDaniel and Sterling 1979), other Heliothis spp., and the boll weevil Anthonomus grandis grandis Boheman (Sterling et al. 1979). Sterling (1978) found that fire ants spread uniformly and in high densities throughout east Texas cotton fields; S. invicta populations increased as the cotton season progressed such that up to 85% of the boll weevil populations were preyed upon. Mirex-induced exclusion of S. invicta in other cotton fields suffered 38.8% boll weevil damage while untreated cotton sustained only 16.6% damage (Jones and Sterling 1979).

Heptachlor exclusion of ants in rice resulted in rice stinkbug Oebalus pugnax F. levels 4 X higher than encountered in untreated fields (this required additional chemical measures) (Newsom et al. 1959), and significant increases in earwig (Gross and Spink 1969) and leafhopper populations (Wilson and Oliver 1969). Research methods that employed heptachlor exclusion of S invicta were extensively utilized in sugarcane where significant sugarcane borer Diatraea saccharalis F. damage resulted (Long et al. 1958, Hensley et al. 1961, Negm and Hensley 1967, Negm and Hensley 1969). Mirex treatments in sugarcane have also demonstrated fire ant suppression of D. saccharalis (Adams et al. 1981, Oliver et al. 1979). Reagan et al. (1972) recorded 53-69% increases in sugarcane borer infestations where mirex was applied. Ali and Reagan

(1985) additionally indicated that floral diversification, by allowing weeds to flourish, resulted in faunal diversification and increased fire ant populations in the sugarcane agroecosystem.

While most agricultural studies pertaining to the fire ant were performed in field crops, positive fire ant attributes were also identified in some tree ecosystems. Where fire ant mounds near pecan trees were killed with acephate drenches, pecan weevils Curculio caryae Horn completed development in 39% of the nuts, but they developed in only 24% where S. invicta was not controlled (Dutcher and Sheppard 1981). Loblolly pine Nantucket pine tip moth, Rhyacionia frustrana Comstock, populations were slightly reduced where fire ants occurred (Wilson and Oliver 1970).

In yet another agricultural environment, Morrill (1977) studied the fire ant in greenhouses where it foraged on whiteflies, Trialeurodes vaporarum Westwood, without appreciably reducing their numbers. In a similar greenhouse experiment, Morrill (1978) demonstrated that S. invicta suppressed the alflafa weevil, Hypera postica Gyllenhal, by 99.6% and pea aphids, Acyrthosiphon pisum Harris, by 100%. Other citations regarding the relationships of the fire ant and the environment are available in Banks et al. (1978), Wojcik (1982) and Wojcik and Lofgren (1986).

CONCLUSIONS

The fire ant is an organism equipped with a great potential for intrinsic rate of natural increase and dispersal, a painful sting, organized foraging habits, and territorial behavior that, in combination, empower it with considerable competitive force in the North

American continent. Since the fire ant's introduction, the biotic community has failed to restrict its encroachment into new areas. Expenditures of $10 million annually in Florida (Lofgren et al. 1975) and many millions in federal and state funds for fire ant control research (Lofgren et al. 1975, Oliver et al. 1979), including the screening of over 2050 chemical formulations among all insecticide categories, attempted chemical applications by ground and air (Lofgren et al. 1975), and even soil disruption methods (Blust et al. 1982), all have all proved impractical or ineffective (Lofgren et al. 1975, Blust et al. 1982, Stimac 1983, Lofgren 1986). Research on bait toxicants was initiated as early as 1939, but only four baits were candidates to be registered for fire ant control at the end of 1986 (Williams 1986). As a result of man's failure to eradicate S. invicta, the ecology of the fire ant's new habitat has been altered with particular regard to other insect communities. While this development in the evolution of faunal composition may be perceived as negative, the manipulation of S. invicta may also prove agriculturally desirable for the biological suppression of key insect pests. As the fire ant appears unaffected by man's attempts to eradicate or restrict its range, both of our respective species are committed, at present, to coexist in the southeastern United States. The possible impact of S. invicta on agriculture has yet to be fully explored and the potential of the fire ant as a beneficial component of our ecosystem may, upon further investigation, reveal additional advantages to its accidental introduction.

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APPENDIX B

THE VERSATILITY OF RADIOTRACER METHODS FOR STUDYING INSECT ETHOLOGY AND ECOLOGY

The following chapter has been submitted to the Florida Entomologist Student Symposium as manuscript number 87-17-1568.

INTRODUCTION

Insect ethology and ecology studies often involve lengthy experiments in conditions that may preclude visual observations. To accurately assess insect behaviors such as dispersal, subterranean habits, feeding, and complex ecological relationships among diversified taxa, an efficient marker is desirable. Useful markers i) are easily applied to large populations, ii) involve minimal manipulation and trauma to the insect, iii) are detectable without destroying or killing the insect samples, iv) are persistent in the insect or community, and v) do not affect the physical or behavioral functions of the labeled organisms (Bugher and Taylor 1949). A review of the literature has revealed an arsenal of marking methods used by behavioral and ecological entomologists. While most tags were effective for their respective purposes, radiotracers enhance their potential usefulness as a research tool in contrast to conventional labeling procedures.

CONVENTIONAL LABELING METHODS

Visual detection

Visually detected markers commonly suffer limitations. Mirenda and Vinson (1979) evaluated 3 methods for tagging the fire ant, Solenopsis invicta Buren: wire ties, paint, and clipped legs. Securely fastened wire ties were retained, but the process of attachment was laborious and required anaesthetization of the ants. Workers with excised legs were killed by their nestmates, and painted labels were scraped off. Fluorescent dye in noninjurious concentrations was retained by only 26-60 percent of treated hornflies, Haemotobia irritans L., and was frequently lethal (Chamberlain et al. 1977). Individually applied

external labels inflict trauma upon the insect and are impractical in lieu of other options (Service 1976). Dusts and dyes have been used to easily label large numbers of insects (Dalmat 1950, Sheppard et al. 1973, Chamberlain et al. 1977). These labels, however, may be lost (Dow 1971, Chamberlain et al. 1977), are suitable only between molts (Arnason et al. 1950), and are not reliable for monitoring species with cryptic habits (Traniello et al. 1985). External markers, thus, are usually of little value for studying insect behavior over long periods of time, for researching trophallaxis (food exchange in social insects), and for unraveling trophic webs. Service (1976) suggested that, in addition to affecting survival rates, paints and powders might make mosquitoes more susceptible to predation.

Internal labels such as dyes ingested by fire ants were used to monitor the intracolony exchange of oil, protein, and carbohydrate foods; however, detection of the label required the destruction of the insects while the dye was extracted, partitioned, and dried before light wavelength absorbance was measured (Vinson 1968). Wilson et al. (1971) tagged fire ants with ingested dyes and detection was only accomplished by crushing the ants on white paper. Brian and Abbott (1977) dissected ants, Myrmica rubra L., to detect dyes. It is difficult to detect dyes and vital stain indicators in small quantities (Hamilton 1935), whereas the sensitivity of radiation detection exceeds that of most chemical and physical methods (to illustrate, carrier-free tritium at 30 Ci per mmole can be diluted by a factor of 10^{12} without hindering detection) (Wang et al. 1975). Showler et al. (1988) diluted 200 μCi Zn-65 in 20 ml molasses to label an entire fire ant colony. The tracer was detectable in the ants six months after the tagged bait had been removed.

Rubidium

Stable (nonradioactive) rubidium (Rb) markers possess unique characteristics relative to visually detected labels. Rubidium can be ingested from labeled artificial diet (Stimmann et al. 1973; Graham and Wolfenbarger 1977), from Rb solutions sprayed onto host plants (Berry et al. 1972, Stimmann 1974, Shepard and Waddill 1976) and from host plants raised from Rb-treated seeds (Cheshire et al. 1987). Frazer and Raworth (1974) labeled pea aphids, Acythosiphon pisum Harris, that had fed on bean plants cultured in Rb-tagged nutrient solutions. Rubidium was detectable by atomic absorption spectroscopy in pea aphids for up to 4 days (77% was eliminated in 2 days) (Frazer and Raworth 1974) and up to 34 days in the adult Mexican bean beetle, Epilachna varivestris Mulsant (Shepard and Waddill 1976). Unlike visually detected markers, ingested Rb can be retained from larval to adult stages as has been demonstrated in the corn earworm, Heliothis zea Boddie (Graham et al. 1978a,b), tobacco budworm, H. virescens F. (Graham and Wolfenbarger 1977), fall armyworm, Spodoptera frugiperda J.E. Smith (Graham et al. 1978a,b), pink bollworm, Pectinophora gossypiella Saunders (Van Steenwyk et al. 1978a,b), cabbage looper, Trichoplusia ni Hubner (Berry et al. 1972, Stimmann et al. 1973), and the imported cabbage worm, Pieris rapae L. (Stimmann 1974); no toxic effects were observed. Stimmann et al. (1973) showed that ingested Rb concentrations of up to 28,000 ppm did not influence adult T. ni fecundity, fertility, longevity, mating behavior, and responses to sex pheromones. Rubidium labels have been successful in flight dispersal studies on the corn earworm, fall armyworm (Graham et al. 1978b), and pink bollworm (Van Steenwyk et al. 1978b), and to trace insect trophic chains (to primary predator level) on grain sorghum

and cotton (Graham et al. 1978a). Despite these advantages, researchers frequently report equivocal results due to variation and detectable levels of naturally occurring Rb in all samples (Stimmann 1974, Shepard and Waddill 1976, Graham et al. 1978b). Further, quantification of Rb requires the physical destruction of samples for the use of atomic absorption spectroscopy or flame emission spectrophotometry (Berry et al. 1972, Graham et al. 1978b, Van Steenwyk et al. 1978a).

RADIOTRACER METHODS

Selection of a radiotracer

A desirable marker i) provides analogs for biologically essential elements (examples: C-14, P-32, Fe-55 and H-3), ii) does not require the destruction of labeled samples, iii) persists in readily detectable quantities for long periods of time, iv) is easily applied to large numbers of insects with minimal manipulation of the populations, and v) may permit detection in the field, even when tagged insects are located underground or within plant material. Unlike Rb, radioactive isotopes (radiotracers) provide biologically essential analogs such as P-32 (Bugher and Taylor 1949, Yates et al. 1951, Radeleff et al. 1952), C-14 (Hilliard and Keeley 1984, Isaac and Rees 1985, Inagaki and Yamashita 1986), H-3 (Bermudez et al. 1985, Kappler et al. 1986, Whitehead et al. 1986), I-125 (Johnson et al. 1984, Ferkovich and Dillard 1986), S-35 (Ishikawa 1984, Wong and Ho 1986), and Ca-45 (Yagi 1958) that can be applied to study such physiological phenomena as reaction rates, metabolic pathways, and the distribution and incorporation of elements or compounds in biological systems (Wang et al. 1975). Radioactive analog or nonanalog nuclides can be administered to monitor the

behavioral and ecological dynamics of individuals, populations, and biotic communities (Odum and Golley 1961). Radiolabeled insects can be detected while living (Lambremont et al. 1977), dead but intact (Lindquist et al. 1951, Dietz and Lambremont 1970, Smittle et al. 1983), or while the insect is functioning in the environment (Rings and Layne 1953, Riegert et al. 1954, Green et al. 1957). Radiotracer techniques offer a wide arsenal of isotopes (Tables 1, 2, & 3) that can be administered and detected in a diversity of ways (Table 1); Jenkins (1961) reported that about 44 different radionuclides were used in entomological studies. To select a radiotracer for labeling insects, several factors must be considered: i) the effective half-life of the isotope in the organism, ii) possible toxic effects to the insect, iii) the type of radiation emitted, iv) the energy of the radiation, v) the form or valence of the radionuclide, and vi) the ease of handling and detecting the label (Jenkins 1961).

The amount of a radioisotope retained by an insect after the administration of a single dose decreases exponentially through time because of both biological elimination and radioactive decay of the radiotracer. The time required for the amount of a particular internalized radiotracer to decrease by one-half in a given insect is termed the effective half-life (Table 2). DiGregorio et al. (1978) reviewed determinations of effective half-lives in insects. Effective half-lives of radiotracers will decrease in response to excretion (Fuller et al. 1954, Rahalkar and Doutt 1965), oviposition (Bugher and Taylor 1949, Rahalkar and Doutt 1965), length of exposure to labeled bait (Sorenson et al. 1980), life stage (Mayer and Brazzel 1961, Crossley 1963) or caste (Spragg and Fox 1974) of the insect, and the

Table 1. Radiotracer uses in insect ecology and ethology experiments categorized by the type of study (mark-recapture population measurements, dispersal and movement, feeding behavior, vector-pathogen relationships, and food chains and webs).

Type of study	Insect or community labeled	Isotope	Mode of Application	Insect stage labeled; detected	Detector[a/]	Reference
MARK-RECAPTURE POPULATION ESTIMATION						
Colony size	Termite Mastotermes darwiniensis Froggatt	La-140	ingested: bait	adult/nymph; adult/nymph	SS	Spragg & Paton 1950
Colony size	Formicid Lasius flavus F.	P-32	dipped	adult; adult	GM	Odum & Pontin 1961
Larval & pupal mortality	Panaxia sp.	S-35	ingested: living deadnettle in labeled nutrient culture	larva; larva/pupa	PRM	Cook & Kettlewell 1960

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
MARK-RECAPTURE POPULATION ESTIMATION (cont'd)						
Population size adults	Mosquito *Culex pipiens* L.	P-32	water culture	larvae; adult	GM	Lindquist et al. 1967
DISPERSAL/MOVEMENT						
Dispersal	Lone star tick *Amblyomma americanum* L.	Fe-59	dipping	adult; adult	-	Schmidt & Smith 1961
Dispersal	Acridid *Melanoplus mexicanus* Sauss	P-32	ingested: bran & molasses	nymph/adult; nymph/adult	GM	Baldwin et al. 1958
Dispersal	Acridids *M. mexicanus* & *Camnula pellucida* Scudder	P-32	ingested: sprayed wheat seedlings	nymph/adult; nymph/adult	PRM	Riegert et al. 1954

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Dispersal	Weevil Conotrachelus nenuphar Hbst.	I-131, Co-60, Sr-89, Zn-65	ingested: water	adult; adult	GM & PRM	Rings & Layne 1953
Dispersal	S. pine beetle Dendroctonus frontalis Zimmermann	P-32	painted on tree boles	adult; adult	PRM	Moore et al. 1979
Dispersal	White pine beetle Pissodes strobi Peck.	Co-60	painted on elytra	adult; adult	PRM	Sullivan 1953
Dispersal	Eur. pine shoot moth Rhyacionia buoliana Schiff.	Co-60	painted on abdomen	adult; adult	PRM	Green et al. 1957

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Dispersal	Blackflies (Simuliidae)	P-32	water culture	larva; adult	auto-radiography	Baldwin et al. 1966
Dispersal	Blackflies	P-32	water culture	larva; larva & pupa	PRM	Fredeen et al. 1953
Dispersal	Mosquitoes *Aedes communis* DeG., *A. pionips* Dyar, *A. excrucians* Wlk., *A. hexodontus* Dyar, *A. punctor* Kirby	P-32	water culture	larva; adult	PRM	Jenkins & Hassett 1951

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Dispersal	Eyegnat *Hippolates pusio* Loew	P-32	ingested: honey	adult; adult	GM	Dow 1959
Dispersal	*Musca domestica* L.	P-32	ingested: milk	adult; adult	-	Schoof & Siverly 1954
Dispersal	*M. domestica*	P-32	ingested: milk	adult; adult	GM	Schoof et al. 1952
Dispersal	Flies *Phanenicia sericata* Meigan, *Phormia regina* Meigan, *M. domestica*	P-32	ingested: aqueous diet	adult; adult	GM	Lindquist et al. 1951

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Dispersal	Walnut husk fly *Rhagoletis completa* Cresson	P-32	labeled attractant on walnut branches	adult; adult	-	Barnes 1959
Dispersal	*Apis mellifera* L.	Au-198	-	adult; adult	-	Courtois & LeCompte 1963
Colony location	Termite *Mastotermes darwiniensis* Froggatt	Sc-46, Au-198	ingested: bait	adult; adult	SS	Spragg & Fox 1974
Location in soil	*Phyllocnistis* sp.	P-32	ingested: sugar-water	adult; adult	-	Sunby 1958
Location in soil	*R. buoliana*	Co-60	painted on abdomen	adult; adult	PRM	Green et al. 1957

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Movement in soil	Wireworm *Agriotes* sp.	Co-60	attached wire	larva; larva	-	Green & Spinks 1955
Movement in soil	Wireworm *Ctenicera destructor* Brown	Co-60	attached wire	larva; larva	GM	Arnason et al. 1950
Movement in soil	White grub sp.	Ta-182	inserted wire	larva; larva	-	Speers 1956
Movement in wood	Carpenter ants *Camponotus* sp.	I-131	ingested: diet	adult; adult	portable SS	Riordan 1960
Crawling behavior	Coccinelid larvae	Ta-182	attached wire	larva; larva	PRM	Banks 1955

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotopes	Mode of application	Insect stage labeled; detected	Detector	Reference
TERRITORIALITY						
	Formicid Formica sanguinea puberula Emery	P-32	injected thistle & ingested from herbivores	adult; adult	-	Pendleton & Grundmann 1954
	Formicid Lasius minutus Emery	P-32	ingested: honey	adult; adult	PRM	Kannowski 1959
	Solenopsis invicta Buren	Mn-54, Zn-65	ingested: molasses	adult; adult	SS	Showler et al. 1987

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
FEEDING BEHAVIOR						
Amount royal jelly consumed	A. mellifera	P-32	ingested:	pre-queen & worker larva; pre-queen & worker larva	LS	Dietz & Lambremont 1970
Amount foods consumed	S. invicta	I-125	ingested: protein, oil, sucrose	adult; adult	-	Howard & Tschinkel 1981b
Assess fire ant crop damage	S. invicta	P-32	ingested: living injected corn, okra, soybeans	adult; adult	LS	Smittle et al. 1983

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Amount vegetation consumed by insects	plants and insects of White Oak Lake bed ecosystem	Cs-137, Sr-90	radioactive waste disposal	plants & insects; plants & insects	gamma spectrometry	Crossley 1961a
Feeding frequency & amount chemosterilant ingested	A. aegypti	P-32	ingested: honey + chemosterilant	adult; adult	-	Schmidt & Smith 1961
Feeding response to repellent	A. aegypti	P-32	ingested: blood + repellent	adult; adult	-	Bar-Zeev & Schmidt 1959

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Feeding response to malathion bait	M. domestica	P-32	ingested: bait	adult; adult	GM	Schmidt & LaBrecque 1959
VECTOR-PATHOGEN RELATIONSHIPS						
Virus trans-mission to plants	Green peach aphid Myzus persicae Sulzer	Po	ingested: diet	nymph/adult; nymph/adult	gold leaf electroscope	Hamilton 1935
Virus trans-mission to plants	Pineapple mealybug Pseudococcus brevipes Ckl.	P-32	ingested: diet	nymph/adult; nymph/adult	auto-radiography	Carter 1945

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Vector-pathogen relationship	mosquito Armigeres obturbans Wlk.	P-32	water culture	larva/adult; Setaria digitata (filarial worm)	auto-radiography	Dissanaike et al. 1957a
Vector-pathogen relationship	mosquito Culex fatigans Say	P-32	water culture	larva/adult; Wucheria bancrofti Cobbold	GM	Dissanaike et al. 1957b
TROPHIC CHAINS & WEBS						
Determine egg predators	Velvetbean caterpillar Anticarsia gemmatalis Hubner	P-32	ingested: honey; trans-ovarial passage	adults to eggs; egg predators	GM & PRM	Buschman et al. 1977

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Determine egg predators	Heliothis virescens F.	P-32	injection of adults: trans-ovarial passage to eggs	eggs; predators	GM	McDaniel & Sterling 1979
Determine egg & larvae predators	H. virescens	P-32	ingested: adults passed label to eggs and larvae	eggs & larvae; predators	-	Moore et al. 1974
Determine larvae & pupae predators	Winter moth Operopthera brumata L.	C-14	ingested: sucrose solution	larvae & pupae; predators	GM	Frank 1967

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Determine egg & larvae predators	*Heliothis* spp., *Pseudoplusia includens* Wlk., *A. gemmatalis*	P-32	Injection of adults: trans-ovarial passage to eggs & larvae	eggs, larvae; predators	auto-radiography	McCarty et al. 1980
Determine larvae & pupae predators	*Aedes stimulans* Wlk. *A. trichurus* Dyar	P-32	water culture	larva; aquatic predators	-	Baldwin et al. 1955
Determine predators	*Aedes communis* DeG., *A. pionips* Dyar, *A. excrucians* Wlk., *A. hexodontus* Dyar, *A. punctor* Kirby	P-32	water culture	label passed to adult; predators	portable rate meter	Jenkins & Hassett 1951

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Determine larvae predators	Blackflies (Simuliidae)	P-32	water culture	larva; predators	PRM	Fredeen et al. 1953
Label internal parasites	Pieris rapae crucivora L.	Ca-45, P-32	ingested: cabbage	larva; parasites (nematodes, fungi)	-	Yagi 1958
Trophic chain	Balsam fir Abies balsamea L.→spruce budworm Choristoneura fumiferana Clemens larvae→predators	P-32	injected balsam fir roots	----------	gas-quenched proportional detector	Krall & Simmons 1977

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Trophic web	Thistle Cirsium undulatum Nutt.→ herbivores→predators	P-32	injected thistle	----------	-	Pendleton & Grundmann 1954
Trophic web	Insects on Heterotheca sp., Rumex sp., & Sorghum halpense L.	P-32	sprayed on foliage	----------	GM	Odum & Kuenzler 1961
Trophic web	White Oak Lake bed ecosystem	Cs-137, Sr-90	radioactive waste disposal	----------	gamma spectrometry	Crossley 1961b
Trophic web	Doe Run (stream)	Bi-214, Ac-228, Cs-137, Sr-90	radioactive waste disposal	----------	SS	Minckley et al. 1961

Table 1. (cont'd)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stage labeled; detected	Detector	Reference
Trophic web	West Branch of Sturgeon River	P-32	dripped into river	----------	-	Ball 1961
Trophic web	lake	Zn-65	sprayed onto lake	----------	SS & GM	Bachmann 1961

a/ GM = Gieger-Muller tube, LS = liquid scintillation detector, SS = solid scintillation detector

PRM = portable rate meter, - = detector not indicated in reference.

Table 2. A representative list of radioisotopic biological half-lives in selected insect taxa[a/].

Insect[b/]	Isotope	T-effective[c/]	Reference
ISOPTERA			
Mastotermes darwiniensis	Sc-46		Spragg & Fox 1974
Froggatt: workers		1-1.5 days	
soldiers		5 days	
Reticulotermes flavipes Kol.	Cs-137	12 days	Rosengaus et al. 1986
R. flavipes	Mn-54	126 days	Rosengaus et al. 1986
ORTHOPTERA			
cockroach sp.	P-32	14 days	Babers et al. 1956
Melanoplus differentialis	Cs-137	2 days	Crossley & Schnell 1961
Thom.	Sr-85	0.5 days	
M. femur-rubrum DeGeer	Cs-137	1.25 days	Crossley & Schnell 1961
	Sr-85	0.8 days	
COLEOPTERA			
Chrysomela knabi Brown	Cs-137		Crossley 1963
young adult		0.8 days	
old adult		0.3 days	

Table 2. (cont'd)

Insect	Isotope	T-effective	Reference
LEPIDOPTERA			
Sciota sp.	Cs-137	4.6 days	DiGregorio et al. 1978
DIPTERA			
Cochlyomyia hominivorax Coquerel: larvae	P-32	7 days	Radeleff et al. 1952
Musca domestica L.	P-32	0.8 days	Babers et al. 1956
HYMENOPTERA			
Habrobracon juglandis Ashmead	Sr-89	1 day	Grosch & LaChance 1956
Phanerotoma flavitestacea Fisher	P-32	36 days	Rahalkar & Doutt 1965
Solenopsis invicta Buren	I-125	4 days	Sorenson et al. 1980

a/ All isotopes were ingested.

b/ All insects were adults unless other life-stage is indicated.

c/ The effective half-life = biological half-life and radioactive decay.

Table 3. Trophallaxis research on termites, ants, and honeybees using radiotracer techniques.

Insect labeled	Radioisotope	Reference
ISOPTERA		
Cryptotermes brevis Walker	Co-57, Sr-85	McMahan 1963
C. brevis	Co-57	McMahan 1966
C. brevis	C-14	Beard 1974
Kalotermes flavicollis F.	P-32	Alibert 1959
K. flavicollis	I-131, P-32	Gosswald & Kloft 1963
Mastotermes darwiniensis Froggatt	Sc-46	Spragg & Fox 1974
M. darwiniensis	La-140	Spragg & Paton 1980
Reticulotermes flavipes Kol.	Co-60, Cs-137, Mn-54, Sb-124, Sb-125, Se-75, Zn-65	Traniello et al. 1985

Table 3. (cont'd)

Insect labeled	Radioisotope	Reference
R. flavipes	Co-60, Mn-54, Sb-125, Sc-46, Se-75, Sr-85, Zn-65	Rosengaus et al. 1986
HYMENOPTERA (Formicidae)		
Formica integra Nylander	P-32	Wilkinson et al. 1978
F. rufa L.	Au-198	Coutois & LeCompte 1963
Formica spp.	I-131, P-32	Gosswald & Kloft 1963
Formica spp.	P-32	Kneitz 1963a,b
Iridomyrmex humilis Mayr	P-32	Markin 1970
Lasius niger L.	P-32	Lenoir 1974
Solenopsis invicta Buren	I-131	Eisner & Wilson 1958
S. invicta	P-32	Gosswald & Kloft 1960
S. invicta	P-32	Naarman 1963

Table 3. (cont'd)

Insect labeled	Radioisotope	Reference
S. invicta	I-125	Howard & Tschinkel 1980
S. invicta	I-125	Sorenson et al. 1980
S. invicta	I-125	Howard & Tschinkel 1981a,b
S. invicta	I-125	Sorenson et al. 1985
Crematogaster lineolata Sat., *Formica fusca* L., *F. pallidefulva* Mayr, *Pogonomyrmex badius* Latr., and *Solenopsis saevissima* Fr. Smith	I-125	Eisner & Wilson 1958
Pheidole dentata Mayr, *Solenopsis geminata* F. and *S. invicta*	P-32	Bhatkar & Kloft 1977
Pogonomyrmex badius Latr. and 2 *Formica* spp.	I-131	Wilson & Eisner 1957

Table 3. (cont'd)

Insect labeled	Radioisotope	Reference
HYMENOPTERA (Apidae)		
Apis mellifera L.	P-32	Nixon & Ribbands 1952
A. mellifera	C-14	Oertel et al. 1953
A. mellifera	Au-198, P-32	Courtois & LeCompte 1963
A. mellifera	I-131, P-32	Gosswald & Kloft 1963

nature of the labeled food ingested (oil, protein, carbohydrate) (Sorenson et al. 1980). Radioactivity can, however, be easily detected long after the isotope's effective half-life has expired (Radeleff et al. 1952, Fuller et al. 1954, Wang et al. 1975). To minimize loss of the radiotracers in individuals over time, the isotopes may be delivered to insects in a continuous infusion by providing a constant supply of radiolabeled food or water (Jenkins and Hassett 1951, Bachmann 1961, Showler et al. 1987), or by using large, but nontoxic, doses of radionuclides in a single pulse application (Wang et al. 1975).

A radiolabel may prove detrimental to the inoculated system (and researcher) due to the nature of the emitted radiation (Wang et al. 1975). The biological hazards of radiation, although negligable in most radiotracer studies, have been magnified by the news media; thus the decline in radioecology experiments after the early 1960's. Radiotracers have received wide application in the study of insect biochemistry and physiology (Odum and Golley 1961, Yates et al. 1951, Grosch and Sullivan 1952, Yagi 1958). In the case of Aedes aegypti L., females were twice as radioactive as males (Bugher and Taylor 1949) such that radiotracers, in excessive quantities, can adversely affect each sex to different degrees within a species. Toxic levels of Ca-45, Fe-59, Ag-110, Cd-115, and I-131 in certain insect species have been documented (Jenkins 1961). Depending on the radioisotope, the dose of radiation delivered, the type of radiation, the insect species and life stage exposed, and the method of radionuclide administration, radiation levels necessary to produce toxic effects may differ. Toxicity may also result from a species-dependent overdose of the stable element itself if the radionuclide is not carrier-free (Wang et al. 1975).

White pine weevils, Pissodes strobi Peck., painted with 500 μCi Co-60 per individual did not suffer increased mortality for at least 2 months (Sullivan 1953), whereas boll weevil, Anthonomus grandis Boheman, mortality increased when P-32 concentrations exceeded 9.9 μCi per gram of labeled diet (Mayer and Brazzel 1961). Mortality studies on termites, Reticulitermes flavipes Kollar, revealed that while equivalent amounts of Mn-54, Sr-85, and Sr-85 + Co-60 produced lethal effects, Co-60, Cs-137, Sb-125, Mn-54 + Zn-65, Mn-54 + Se-75, Co-60 + Cs-137, and Cs-137 + Se-75 were benign (Traniello et al. 1985). In contrast, Grosch and Sullivan (1952) found that Habrobracon juglandis Ashmead developed "radioresistance"; P-32-treated adults survived as long or longer than controls. Sublethal doses of radiation have been shown to incur damage by reducing insect fecundity (Bugher and Taylor 1949, Blumel 1950). H. juglandis adults fed on less than 50 μCi P-32 per gram of labeled food displayed no ill-effects; 50-200 μCi resulted in decreased (ca. 26 percent) egg production, and 200 μCi halted the process entirely (Grosch and Sullivan 1952). Eggs produced from radiolabeled adults may also show increased mortality (Banks 1955, Babers et al. 1956) and offspring hatched from labeled eggs may be deformed or die soon after eclosion (Blumel 1950, Banks 1955). Mayer and Brazzel (1961) demonstrated, further, that A. grandis larvae raised on P-32-labeled diet developed into adults with adversely affected longevity, fecundity, and pre-oviposition and ovipositional periods when compared with adults fed on similarly tagged diet. Radiotracer levels, however, may not hinder longevity, fecundity, fertility, or egg eclosion as demonstrated by P-32 assays on the screw-worm fly, Cochliomyia hominivorax Coquerel (Radeleff et al. 1952). Thus the use of a fixed radionuclide dose may be suitable

for one species but impractical for another (Jenkins 1961). If the radionuclide is administered in a nontoxic dose, any species can be radiolabeled.

Those nuclides that dissipate energy as gamma photons possess advantages peculiar to the nature of gamma radiation. Gamma-emitting isotopes produce characteristic spectral emission "signatures" such that confusion between different radionuclides in the same insect or community is eliminated (Traniello et al. 1985, Showler et al. 1988). Additionally, because gamma rays have negligible mass and are extremely penetrating, gamma-emitting isotopes have been employed to locate cryptic insects through several cm of soil (Tomes and Brian 1946, Arnason et al. 1950) and up to 14 cm of wood (Riordan 1960).

Radiolabeling methods

There is a diversity of methods by which radiotracers have been introduced to insects (Jenkins 1961). Radiotracers can be applied as components of biologically essential compounds for biochemical research (Wang et al. 1975), and A. aegypti sperm has been labeled with P-32 developed for mating studies (Schmidt and Smith 1961). Insect ethology and ecology research is less specific regarding the chemical form of the administered nuclide. The following labeling techniques have been used to tag individuals (Odum and Pontin 1961, Tomes and Brian 1946), populations (Spragg and Fox, 1974, Showler et al. 1987), or entire biotic communities (Bachmann 1961, Crossley 1963):

A. Dipping and painting. Dipping insects in radioactive solutions has been successfully implemented to mark individuals. The lone star tick, Amblyomma americanum L., was dipped in an Fe-59 suspension to investigate dispersal in pastures (Schmidt and Smith 1961); I-131, Se-46, Ir-192 (Davis and Nagel 1956), and Co-60 (Sullivan 1953) dips were successful for tracing Englemann spruce weevils, P. strobi, (Davis and Nagel 1956) and for A. grandis (Babers et al. 1954). The addition of a detergent allowed a P-32-labeled water dip to penetrate the cuticle of the ant Lasius flavus F. for a retention time of 10 days (Odum and Pontin 1961). Phosphorus-32 dipping of the plum curculio, Conotrachelus nenuphar Hbst., was not effective (rate of success not given) despite supplementation with wetting and sticking agents (Rings and Layne 1953). Phosphorus-32-glycerin suspensions painted onto the southern pine beetle, Dendroctonus frontalis Zimmermann, permitted the location of tagged beetles after dispersal by the presence of P-32 on host tree pitch tubes (Moore et al. 1979). D. frontalis adults were also labeled with paint (100 percent effective) as they emerged from tree boles which had been painted with P-32 (Moore and Taylor 1976). Painted radiolabels, like many visual markers, can be chipped or washed off, and thus may give false indications of radioactivity in the environment (Green et al. 1957).

B. Radioactive Disc and wire attachments. The movements of various subterranean beetle larvae have been monitored with external disc or wire attachments labeled with Ra-226 (Tomes and Brian 1946), Ta-182 (Speers 1956), and Co-60 (Green and Spinks 1955). Similarly, Ta-182 wire glued to coccinelid larvae was used to investigate crawling

behavior on foliage (Banks 1955). Discs and wires glued or tied to the insect exoskeleton or inserted within the insect's body suffer the disadvantages previously described for some visually detected markers such as individual and manual tagging and subsequent trauma to the organism being studied.

C. Ingestion. Isotopes are effectively transferred to insects by ingestion of radiolabeled food; in this way, large numbers of marked insects can be reared simultaneously. See Table 1 for a representative list of various ingested radiolabeled materials. Tagged sugar and honey solutions (Grosch and Sullivan 1952, Baldwin et al. 1958), artificial diets (Babers et al. 1956, Mayer and Brazzell 1961, Traniello et al. 1985), royal jelly (Dietz and Lambremont 1970), milk (Babers et al. 1956), and living plants smeared or sprayed with radiotracers (Fuller et al. 1954, Crossley and Schnell 1961, Odum and Kuenzler 1961) have produced good results in a variety of insects. Labeled wood, blood, and living insect prey have been employed to tag termites (McMahan 1963), mosquitoes (Bar-Zeev and Schmidt 1959), and mantids (Jenkins and Hassett 1950), respectively.

A more refined radiolabeling technique involves rearing insects on plants cultured in radiotagged nutrient solutions (Cook and Kettlewell 1960) or plants injected with radioisotopes (Beckman and Kuntz 1951, Fraser and Mawson 1953, Graham 1954). Insect trophic webs on the thistle, Cirsium undulatum Nutt. (Pendleton and Grundmann 1954), and balsam fir, Abies balsamea L. (Krall and Simmons 1977), were determined by injecting these plants with P-32. Similarly, P-32 injected into living rats and rabbits, goats and sheep, and hamsters resulted in the

successful tagging (exact rates not given) of A. aegypti (Jenkins and Hassett 1950), screw-worm flies (Radeleff et al. 1952), and Oriental rat fleas Xenopsylla cheopis Rothschild (Jenkins 1957), respectively.

Several trophic level interaction studies have been conducted in the White Oak Lake bed, an area in South Carolina contaminated by Cs-137 and Sr-90 wastes that were subsequently translocated by the terrestrial plant community (Crossley 1961b, Crossley 1963). The trophic web of a stream was studied using naturally occurring U-238 and Th-232 fission-products Bi-214 and actinium-228 (Minckley et al. 1961).

D. Water culture. Large quantities of aquatic insects such as mosquitoes and blackflies have been labeled through adulthood when the larvae were raised in P-32-tagged water (Yates et al. 1951, Fredeen et al. 1953, Baldwin et al. 1966); Yates et al. (1951) and Fredeen et al. (1953) reorted that 100% of the adults acquired the P-32. In a large-scale application of this technique, Zn-65 was sprayed onto a lake (Bachmann 1961), and P-32 was systematically dripped into a stream (Ball 1961) to evaluate the trophic structure of each system.

E. Trans-life-stage transmission. To further illustrate the versatility of radiotracer application to insect populations, radioisotopes are transferred through different life stages of the same insect. This phenomenon has been observed when the initially labeled insect stage obtained the tag by injection (McDaniel et al. 1978), ingestion (Kettlewell 1952, Moore et al. 1974), or radiolabeled water culture (Jenkins and Hassett 1951, Yates et al. 1951, Baldwin et al. 1966). Grasshoppers Melanoplus mexicanus Sauss and Camnula pellucida

Scudd. were shown to pass ingested P-32 from nymphal to adult stages (Fuller et al. 1954). Similarly, larvae labeled via ingestion retained S-35 to adulthood in Panaxia sp. and Arctia caja L. (Kettlewell 1952), Ca-45 and P-32 in P. rapae (Yagi 1958), and P-32 in A. grandis (Mayer and Brazzell 1961). Screw worm fly larvae raised on P-32-injected goats and sheep passed detectable tracer levels to pupae, adults, eggs, and the next larval generation (Radeleff et al. 1952). Adult insects that had ingested radiotagged food transferred the label to their eggs; examples include Sr-89 in H. juglandis (Grosch and LaChance 1956), and P-32 in the walnut husk fly, Rhagoletes completa Cresson, (Barnes 1959) and the velvetbean caterpillar, Anticarsia gemmatalis Hubner (Buschman et al. 1977). Furthermore, P-32 may be transmitted from adult to egg to larva, as exemplified in H. virescens (Hines et al. 1973, Moore et al. 1974). Larval mosquitoes and blackflies raised in P-32-labeled water cultures retained the tag into adulthood (Jenkins and Hassett 1951, Yates et al. 1951, Baldwin et al. 1966). Smittle et al. (1973) found that first and second egg batches of Culex pipiens L. retained P-32 from individuals raised as larvae in a labeled water culture.

Methods of detection

Recognition of different methods for radiation-detection adds another dimension to the versatility of radiotracer application. The detector of choice may depend upon the type of radiation to be measured, the physical state of the sample, and whether or not detection will occur in the laboratory or the field (Wang et al. 1975, Service 1976). Wang et al. (1975) described the different detectors available, of which the Gieger-Muller tube (Linquist et al. 1951, Schoof et al. 1952, Dow

1959), liquid scintillation (LS) detector (Auerbach et al. 1964, Dietz and Lambremont 1970), solid scintillation (SS) detector (Spragg and Paton 1980, Traniello et al. 1985, Showler et al. 1987), autoradiography (Baldwin et al. 1966, Markin 1970), and portable rate meters (Fuller et al. 1954, Taylor and Moore 1978) have received greatest use in insect ethology and ecology studies. Portable rate meters are useful for the detection of labeled insects encountered in the environment and have been employed to locate P-32 (Riegert et al. 1954, Moore et al. 1979), Co-60 (Sullivan 1953, Green et al. 1957), I-131 (Rings and Layne 1953, Riordan 1960), Sr-89 and Zn-65 (Rings and Layne 1953), and Ta-182 (Banks 1955) in insects, some located inside soil (Tomes and Brian 1946, Arnason et al. 1950) or wood (Riordan 1960).

Cerenkov radiation (Wang et al. 1975) can be measured from within living insects placed in a liquid scintillation detector (Lambremont et al. 1977). See Table 1 for a more extensive review of detector types used to measure radioactivity in insect ethology and ecology experiments.

Fields of application

Odum and Golley (1961) listed areas of study within insect ecology and ethology to which radiotracer methods have been applied; these fields were population measurements, dispersal and movement, feeding behaviors, and trophic webs. In light of more recent discoveries, the above list should be amended to include territoriality and vector-parasite relationships. Representative implementations of radiotracer studies in ethological and ecological entomology are summarized in Tables 1 and 3.

A. Population measurements. Mark-recapture statistical methods (Southwood 1966, Steele and Torrie 1980) and radiolabeled population members have been employed to estimate the numbers of ants Lasius flavus F. (Odum and Pontin 1961) and termites Mastotermes darwiniensis Froggatt (Spragg and Paton 1980) per colony. Lindquist et al. (1967) used P-32 to estimate the population size of Culex pipiens in Rangoon, Burma. Insects that exhibit trophallactic behavior distribute ingested labels among other individuals to render mark-recapture efforts invalid. Because a relatively large proportion of the studied population should be marked to obtain a high rate of recaptures (Mosby 1969, Seber 1973), radiotracers are suitable markers.

B. Dispersal and movement. Numerous researchers have investigated the dispersal of a variety of insects such as D. frontalis (Moore et al. 1979), blackflies (Fredeen et al. 1953, Baldwin et al. 1966), mosquitoes (Jenkins and Hassett 1951), Musca domestica L. (Schoof et al. 1952, Schoof and Siverly 1954), acridids (Riegert et al. 1954, Baldwin et al. 1958), weevils (Rings and Layne 1953, Sullivan 1953), honeybees (Courtois and LeCompte 1963), and moths (Green et al, 1957). A review of the literature revealed that the greatest weakness of dispersal experiments was in the sampling for the insects after they had moved into the environment. More extensive reviews on mosquito (Jenkins 1954, Jenkins 1961, Service 1976) and housefly (Jenkins 1954) dispersal studies demonstrate the successful application of radiotracers to such mobile and economically important insects. Insect movement patterns in soil (Green and Spinks 1955), wood (Riordan 1960), and on foliage (Banks 1955) have been investigated with radionuclides.

C. Territoriality. Social insects provide models for the study of territorial behavior. Pendleton and Grundmann (1954) injected a thistle C. undulatum with P-32; ants Formica sanguinea puberula Emery acquired the label from the thistle by foraging on radioactive honeydew excreted by aphids. Because nearby F. puberula colonies remained unlabeled, intraspecific territorial behavior was suggested. Similarly, P-32-labeled L. minutus colonies were shown to be discrete from other colonies of the same species (Kannowski 1959). More direct evidence for territorial behavior was demonstrated by Showler et al. (1987); two adjacent fire ant colonies, one labeled with Zn-65 and the other with Mn-54, were monitored. Territorial patterns were clearly delineated during 21 consecutive days.

D. Feeding behavior. Amounts of various food sources consumed by insects can be measured with radiotracers; examples include P-32-labeled royal jelly by honeybee larvae (Dietz and Lambremont 1970), and I-125-labeled protein, oil, and sucrose by fire ants (Howard and Tschinkel 1981a,b). Fire ant consumption of P-32-labeled corn, soybeans, and okra was assessed by analyzing the ants for radiation (Smittle et al. 1983). A complex application of this technique was undertaken by Crossley (1961a) to estimate the feeding rate of the herbivorous insect fauna in the Cs-137- and Sr-90-contaminated White Oak Lake bed ecosystem. Modification of such experiments permitted evaluation of A. aegypti feeding responses to chemically altered food sources such as repellents (Bar-Zeev and Schmidt 1959) and chemosterilants (Schmidt and Smith 1961) in blood, and houseflies to malathion baits (Schmidt and LaBrecque 1959).

The study of trophallaxis among social insects has largely relied upon radiotracer methods (Table 3). Naarmann (1963) used P-32 to show that formicid food secretions are primarily formed in the pharyngeal glands, stored in the crop, then regurgitated. Other radiotracer experiments revealed that food exchange rates may be governed by temperature, time, colony size, starvation (Kneitz 1963, Gosswald and Kloft 1963, Howard and Tschinkel 1980), and the food type ingested (Markin 1970, Howard and Tschinkel 1981a,b). Different rates of food exchange were also observed between social castes (McMahan 1963; Sorenson et al. 1985) and life stages (Markin 1970, Howard and Tschinkel 1981). Eisner and Wilson (1958) found that seed-eating Pogonomyrmex badius Latrielle (a "primitive" myrmicine) exchanged I-125-labeled honey-water slowly (rate not given) while the more "specialized" aphid-tending Solenopsis saevissima Fr. Smith trophallactic rate was significantly higher: in 3 days 65% of a colony's adults were labeled. The "very specialized" aphid-tending Crematogaster lineolata Sat. transferred the tracer to 90% of its nestmates within 30 hr.

E. Vector-parasite relationships. The investigation of insect transmission of pathogenic organisms to plant and animal hosts has involved the use of radionuclides. The pineapple mealybug, Pseudococcus brevipes Ckl. (Carter 1945), and the green peach aphid, Myzus persicae Sulzer (Hamilton 1935), were shown to be plant virus vectors using P-32 and polonium, respectively.

Jenkins (1954) indicated that several insect-vectored and medically important pathogens have been radiolabelled; examples include Onchocerca volvulus Leuckart with radioantimony; various protozoa with Fe-55,

Fe-59, and P-32; and Bacillus subtilis, B. coli, Escherichia coli, a virus bacteriophage, and influenza virus with P-32. Moraczenski and Kelsey (1948) reported P-32-labeled Trypanosoma sp. Mosquitoes, Armigeres obturbans Walker and Culex fatigans Say, cultured in P-32-labeled water were found to transfer the tag to microfilarial Setaria digitata Railliet and Henry and Wucheria bancrofti Cobbold (Dissanaike et al., 1957,a,b), which suggested that there was a trophic relationship between the insect vectors and the pathogens.

F. Trophic chains and webs. Radiotracer methodology has enabled entomologists to identify predators of various economically important insects. Baldwin et al. (1955) produced tagged Aedes stimulans Wlk. and A. trichurus Dyar larvae from P-32-labeled water. After the larvae were transferred to ponds, predatory insect samples revealed that Limnephilus indivisus Walker, Stagnicola palustris Muller, Gerris spp., Gyrinus lecontei Fall, Hydrophilus obtusatus Say, Glossiphonia fusca Castle, Belostoma fluminea Say, Ronatra fusca Beauv., and Callicorixa audeni Hung. were radioactive. The amount of radiation per predator indicated the approximate numbers of culicid larvae consumed. Phosphorus-32-labeled H. virescens eggs were used to identify egg predators in cotton such as S. invicta, Orius insidiosus Say, Geocoris punctipes Say, G. uliginosus Say, Pseudatomoscelis seriatus Reuter, Hippodamia convergens Guerin-Meneville, Cycloneda sanguinea L., Coleomegilla maculata DeGeer, Scymnus loewii Mulsant, Heliothis spp. larvae, Peucetia viridans Hentz, Oxyopes salticus Hentz, and Misumenops spp. (McDaniel and Sterling 1979). Similarly, internal parasites of P-32-tagged P. rapae larvae, such as nematodes and fungi, obtained the label (Yagi 1958).

Radiotracers can be passed from injected plants to herbivores and on to predators (Krall and Simmons 1977, McCarty et al. 1980) and symbiotes (Pendleton and Grundmann 1954). Trophic webs in large-scale complex ecosystems have been untangled in areas where radiotracers have been introduced to areas where radioactive waste products have accumulated in the environment (Crossley 1961b, Minckley et al. 1961), or aquatic communities (Bachmann 1961, Ball 1961). Relative proportions of isotopes may differ from one organism to another because of dissimilarities in the chemical composition and physiological demands of the different taxa, different sorption characteristics, variation in moisture content between organisms, and relative position of the species on the food chain (Davis and Foster 1958).

NEUTRON ACTIVATION ANALYSIS

Due to public concern regarding the potential detrimental effects of ionizing radiation, some scientists have turned to neutron activation analysis (NAA) to provide an avenue to avoid this problem (Jenkins 1963) often without the sacrifice of radiotracer sensitivity (Wang et al. 1975). Wang et al. (1975) listed the large selection of available stable-activable markers. Rare earths, such as Sm and Dy, are good physical tracers but are not analagous to biochemically essential elements. Because stable-activable markers are made radioactive by exposing samples to specific thermal neutron fluxes in a nuclear reactor (Wang et al. 1975, Knaus and Curry 1979), the thermal neutron capture cross-section of the nuclide should be large ($\geq$ 0.1 barn). The natural abundance of the stable tracer in the experimental system should be less than 10% of the applied dose to avoid equivocal results (Wang et al.

1975) such as those encounteredwith Rb labels. The NAA tracer for insect ethology and ecology studies should be selected for a short half-life and readily detected radiations (preferably gamma rays) after the nuclide has been activated (Wang et al. 1975, Southwood 1978). NAA methods provide radio-safety in the environment, a diversity of nuclides from which to choose, and sensitivity of detection. The technique also permits long-term experiments without decay of the tracer, nondestructive sample analysis such that the same sample can be repeatedly activated and measured (Wang et al. 1975, Knaus and Curry 1979), and quantification of the label in each sample based upon the amount of radiation emitted (Knaus and Curry 1979). Drawbacks to NAA techniques include i) relatively long (≧ 1 day) analyses of samples (Wang et al. 1975, Knaus and Curry 1979), ii) persistence of the stable tracer in the environment which may render future experiments in the same area unreliable (Wang et al. 1975), and iii) "loss" of the tracer in the experimental system until NAA is performed (Knaus and Curry 1979). The activated nuclide can be detected and quantified using the same diversity of methods available for conventional radiotracers (Wang et al. 1975).

While toxicity to the insect may result from stable-activable tracers, detectable nonlethal levels may be attained by experimentation (Curtis et al. 1973). Application of these nuclides to the insect has been achieved through ingestion (Richardson 1969, Richardson et al. 1971, Curtis et al. 1973) and by the absorption of cerium into the cuticle of palm weevils Rhynchophorus sp. (Rahalkar et al. 1971). White mustard, Brassica hirta Moench, and hairy vetch, Vicia villosa Roth, have been shown to translocate Dy and Eu from soil to leaves (Kloke and

Riebartsch 1965); thus certain herbivorous insects may be labeled on tagged host plants, and, by extension, trophic webs could be examined using NAA techniques.

At present, NAA has not received great attention in entomology. Curtis et al. (1973) successfully tagged the tsetse fly, Glossina morsitans Westwood, with Eu-, Dy-, Au-, and Ir-labeled nutrient solutions. Dysprosium was shown to be a life-long marker in Drosophila spp. (Richardson et al. 1969) and was employed for dispersal studies (Richardson 1968). Manganese ingested by the Mediteranean fruit fly, Cerititis capitata Wied, was detectable with NAA (Monro 1968). NAA allows the precise measurement of dispersal patterns that reveal behavioral parameters, ecological components, and rates and other characteristics of movement and reproduction with little disturbance to individual behaviors, population structures, and ecological systems (Gage et al. 1969). A more complex implementation of NAA involved Sm-labeled bait to tag fire ants in a Louisiana sugarcane field to observe the territorial areas of 6 colonies (Showler et al. 1987).

Other activation analysis methods have been conducted with trace elements and compounds such as zirconium oxide, Bi, Pb, cerium oxide, Sn, and Se sprayed on mosquitoes then bombarded with alpha particles in a cyclotron to produce X-ray emissions (McClelland et al. 1973a). In a field trial, however, Aedes nigromaculis Ludlow adults did not retain detectable levels of the topically applied alpha-activable tracers (McClelland et al. 1973b). Service (1976) suggested the use of high energy X-rays to interact with natural trace elements in mosquitoes to elicit fluorescent X-rays that are proportional to the atomic weights of the "marker" trace elements in the sample.

CONCLUSIONS

Radiotracer methods and INAA provide researchers of insect ecology and ethology with versatile and sensitive tools relative to conventional labeling procedures. Applications of radioactive isotopes, when evaluated through the appropriate feasibility studies, can avoid the pitfalls of conventional labeling techniques. Radiotracers are easy to apply to large insect populations, minimize direct manipulation and trauma to individual insects, are detectable in the field or lab without killing or destroying the samples, can persist at detectable levels in the insect or community, and do not necessarily alter the physical or behavioral nature of the labeled organisms. Although conventional tagging methods have been shown to be effective for dispersal (Dalmat 1950, Reeves et al. 1948), territorial (Wilson et al. 1971), and feeding (Berry et al. 1972, Raworth 1974, Stimman 1974, Shepard and Waddill 1976) studies, radiotracer labeling, as a single methodology, provides greater flexibility with regard to modes of application, detection, and the types of studies to be conducted. Judiciously employed combinations of available radiotracer techniques could reveal a wide spectrum of behavioral and ecological information unattainable with alternative methods. It is conceivable that a single, well-planned radiotracer and/or NAA experiment could provide information relevant to insect population structures, dispersal and movement, territoriality, feeding behaviors, reproductive strategies, and various physiological phenomena. Prudent use of radiotracer and NAA technology could equip research with the capacity to expediciously enhance current perceptions of insect interactions with man and the environment.

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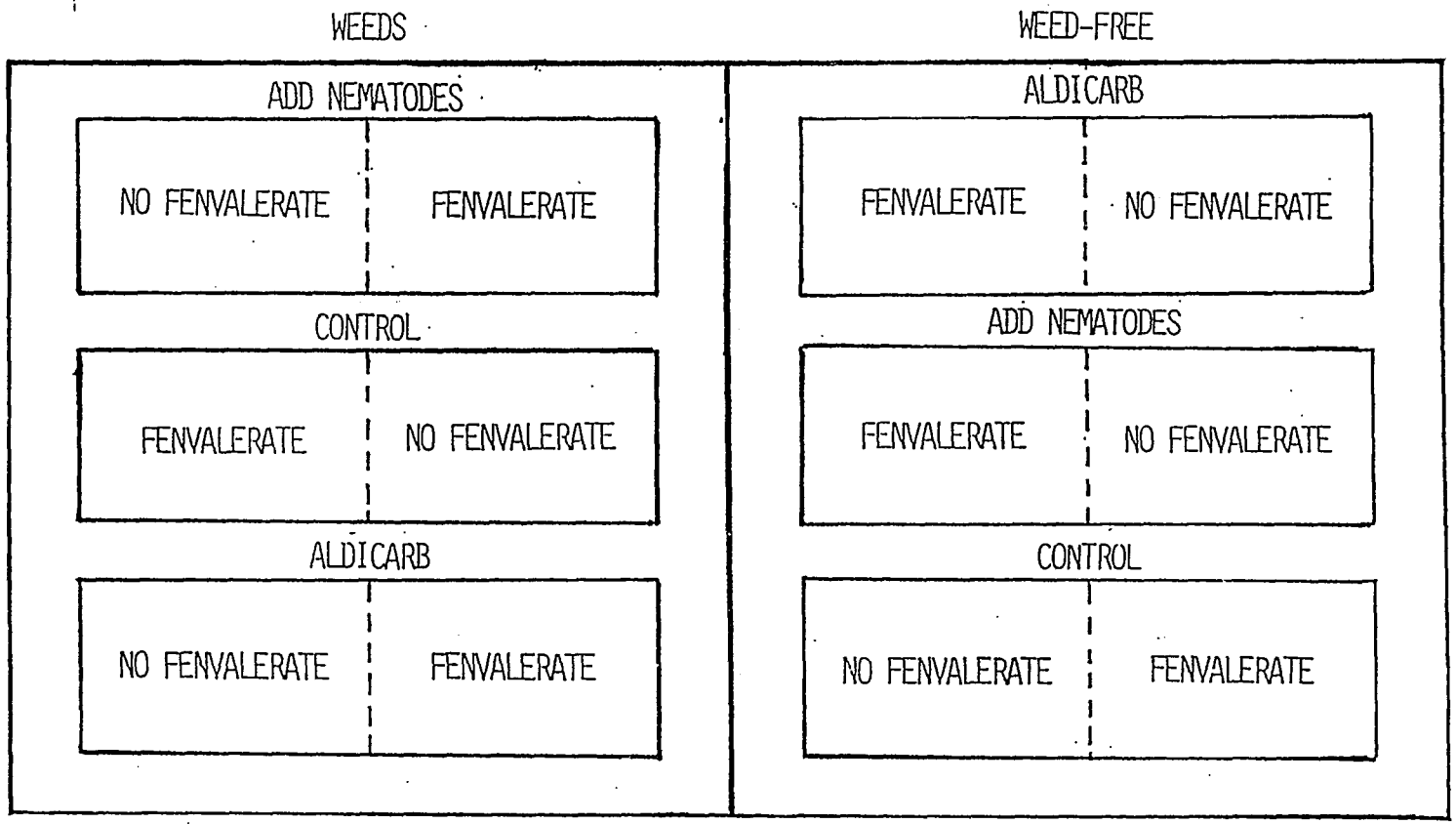
APPENDIX C

Diagram of the randomized complete block design with a split-split plot arrangement of treatments in the six acre sugarcane (CP 74-383) field at Westfield Sugar Plantation, Assumption Parish, Louisiana, 1985 and 1986.

1 REPLICATION WESTFIELD SUGARCANE EXPERIMENT



There were six replicates; each replicate was 0.4 ha in area. Sub plots were 0.05 ha in area each, and sub-sub plots were 0.025 ha in area, each.

APPENDIX D

Nematode groups found in the sugarcane field at Westfield Sugar Plantation, Assumption Parish, Louisiana.

Phytophagous nematodes

Criconemella curvata (ring)

Criconemella onoensis (ring)

Dorylaimida spp.

Helicotylenchus dihystera (spiral)

Helicotylenchus pseudorobustus (spiral)

Hoplolaimus columbus (lance)

Meloidogyne javanica (root knot)

Meloidogyne incognita (root knot)

Paratrichodorus minor (stubby root)

Pratylenchus zeae (lesion)

Tylenchorhynchus annulatus (stunt)

Nonphytophagous nematodes

Various unidentified species

APPENDIX E

Production costs in dollars per hectare for the eight selected sugarcane pest management regimes.

Table 1. Pesticide costs per season in dollars[a/]

Material	Cost $ per unit	Rate	Cost $ per treatment	Number of treatments	Total $ cost
Aldicarb	29.69/kg	0.53 kg/ha	21.04	1	21.04
Asulox	9.25/1	0.62 1/ha	5.72	1	5.72
Fenvalerate	88.84/kg	0.16 kg/ha	14.21	3	42.68
Metribuzin	29.68/kg	1.30 kg/ha	38.58	1	38.58
Weedmaster	4.00/qt	1.00 qt/ha	4.00	1	4.00

[a/] Pesticide costs on a per ha per year basis. Costs were determined in 1987.

Table 2. Costs for the eight pest control strategies used at the Westfield Sugar Plantation, Assumption Parish, Louisiana[a/].

Treatment[b/]	Material $ costs	Application $ costs[c/]	Treatment costs[d/]
WC-NI	0	0	0
WC-I	47.33	23.04	70.37
WFC-NI	88.78	18.62	107.40
WFC-I	136.11	41.66	177.77
WA-NI	23.35	5.18	28.53
WA-I	70.68	28.22	98.90
WFA-NI	112.13	23.78	135.91
WFA-I	159.46	46.82	206.28

a/ Pest control costs were calculated in 1987 on a dollar per ha per season basis.

b/ WC-NI = weedy, no fenvalerate; WC-I = weedy, fenvalerate-treated; WFC-NI = weed-free, no fenvalerate; WFC-I = weed-free, fenvalerate-treated; WA-NI = weedy, aldicarb-treated, no fenvalerate; WA-I = weedy, aldicarb + fenvalerate; WFA-NI = weed-free, aldicarb-treated, no fenvalerate; WFA-I = weed-free, aldicarb + fenvalerate.

c/ Machinery and equipment for pesticide applications: for herbicides, a tractor-spreader, 50-80 hp, disk and pre-emerge rig and boom sprayer; for aldicarb, tractor spreader, 50-80 hp; for fenvalerate, custom aerial application.

d/ Baseline per ha per year cost of maintaining the land was estimated at $653, but was omitted from the listed pest control costs.

APPENDIX F

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October 24, 1987

DEPARTMENT OF ENTOMOLOGY

LOUISIANA AGRICULTURAL EXPERIMENT STATION
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Dr. Harry O. Yates III
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Carlton Street
Athens, GA 30602

Dear Dr. Yates:

I am currently in the process of finalizing my dissertation and would like to include in it my manuscript "Ecological interactions of the red imported fire ant in the southeastern United States," which has been accepted for publication in the Journal of Entomological Science. The Louisiana State University Graduate School policy, in observance of Copyright laws, requires a written permission from the publisher for such use, in order that the dissertation be microfilmed by University Microfilms, Inc. Please note that I intend to use the article as part of a dissertation in the original manuscript format and not as a reprint.

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Sincerely;

A. T. Showler
Graduate Student

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Editor
Journal of Entomological Science
Forestry Sciences Laboratory
Carlton Street
Athens, GA 30605

APPENDIX F

Voucher Specimens

Allan T. Showler, Ph.D. Dissertation, 1987.

All voucher specimens are retained by the Louisiana State University Department of Entomology under the care of Dr. Joan B. Chapin, Professor and Curator of the L.S.U. Entomology Museum.

Family	Scientific name
Pyralidae	Diatraea saccharalis (F.)
Formicidae	Aphaenogaster rudis Emery
	Crematogaster clara Mayr
	Hypoponera opaciceps Mayr
	Monomorium minimum Buckley
	Myrmecina americana Emery
	Paratrechina vividula Nylander
	Pheidole moerens Wheeler
	Solenopsis invicta Buren
	Solenopsis molesta Say

VITA

Allan Thomas Showler was born on November 17, 1956, in Sacramento, California, to Donald Harmon and Gloria Antoinette Showler. He attended La Sierra High School in Carmichael, and after graduation in 1975, enrolled at American River Community College in Sacramento. In the fall of 1977, he transferred to the University of California at Davis, and earned a B.S. degree in Entomology in December, 1979. His M.S. degree in Plant Protection and Pest Management was completed at U.C. Davis in December 1981. During his studies at Davis, Allan worked as a laboratory assistant for entomology research on potatoes in Tulelake and Half Moon Bay, seed alfalfa in the San Joaquin Valley near Firebaugh, and blue tongue virus vectors in the Sacramento Valley, California. In 1982 he volunteered for Peace Corps service and was sited in Ras Djebel and Sfax, Tunisia, as a student of Arabic and as an agricultural extension agent. After returning to California in 1983, he was employed as a research and development scientist for Abbott Laboratories' bacterial insecticides and plant growth regulator compounds in Fresno. In 1984, Allan was awarded a Distinguished Louisiana State University Alumni Federation Fellowship and was admitted to the Ph.D. program in the Department of Entomology at Louisiana State University with minors in Nuclear Science and Experimental Statistics. He is currently completing the requirements for the Ph.D. degree and aspires to contribute to the improvement of agricultural methods in developing regions of the world.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Allan Thomas Showler

Major Field: Entomology

Title of Dissertation: Interactions of Weed, Nematode, and Arthropod Management Strategies with the Louisiana Sugarcane Agroecosystem: A Holistic Perspective.

Approved:

T E Reagan
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

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Date of Examination:

November 23, 1987